THE CHROMOSOMES IN CROSS–FERTILIZED ECHINOID EGGS.

D. H. TENNENT.

In experiments which I carried on during the summer of 1907[1] crosses were made between several echinoids, namely, by the fertilization of :

1. The egg of the spatangoid *Moira atropos* with the sperm of the sand-dollar *Mellita pentapora*.

2. The egg of *Moira* with the sperm of the sea urchin *Toxopneustes variegatus*.

3. The egg of *Moira* with the sperm of the sea urchin *Arbacia punctulata*.

4. The egg of *Toxopneustes* with the sperm of *Moira*.

5. The egg of *Toxopneustes* with the sperm of *Mellita*.

6. The egg of *Arbacia* with the sperm of *Moira*.

7. The egg of *Arbacia* with the sperm of *Mellita*.

8. The egg of *Mellita* with the sperm of *Moira*.

The work was undertaken primarily with the object of obtaining material for a cytological study of cross-fertilized eggs and secondarily for the purpose of making a comparison, based especially upon the character of the skeleton, between larval forms.

In this paper I shall consider some of the earlier phenomena exhibited, in brief, the prophases and early metaphases of division, in two of the crosses, (1), $\dfrac{Moira\ \male}{Toxopneustes\ \female}$ and (2), $\dfrac{Moira\ \male}{Arbacia\ \female}$, reserving the consideration of later stages, of the other crosses, and a general discussion of the results for a latter contribution.

The method of effecting the cross-fertilization was the exceedingly simple one of allowing the eggs, after their removal from the ovary, to stand for several hours in sea water, the water being changed occasionally, and at the most favorable time, which was

determined by experiment, to fertilize the eggs with normally very active sperm.

All attempts at cross-fertilization of the eggs immediately after their removal from the ovary were unsuccessful.

For the $\dfrac{Moira \, \male}{Toxopneustes \, \female}$ crosses the eggs were allowed to stand in sea water for five hours and for the $\dfrac{Moira \, \male}{Arbacia \, \female}$ crosses for seven hours, before fertilization.

Fully 95 per cent. of the eggs so treated underwent a regular and comparatively uniform cleavage, the greater number developing into swimming blastulæ and gastrulæ. About 75 per cent. of these embryos never developed beyond this stage. The remaining 25 per cent. developed into plutei which remained alive and were kept under observation for about ten days.

This high percentage of segmentation was never approached in experiments in which chemicals were employed as aids in effecting cross-fertilization, although naturally no attempts to bring such methods to perfection were made after I had obtained so simple a means of bringing about the results that I desired.

The fact that the eggs were actually fertilized was recognized in the transparent *Toxopneustes* eggs by the observation of the union of the pronuclei. In the cases of both the *Toxopneustes* and *Arbacia* eggs a fertilization membrane was formed.

Each series was checked by a control series of unfertilized eggs. In these controls the eggs were allowed to stand, with occasional changes of sea water, and in every instance the eggs ultimately disintegrated without undergoing segmentation.

The figures that illustrate the account that follows were drawn from sections of picro-acetic and sublimate-acetic material stained in iron hæmatoxylin.

A. THE *Moira* ♂ *Toxopneustes* ♀ CROSS.

The *Toxopneustes* eggs stood in sea water, which was changed four times, for five hours when they were fertilized with *Moira* sperm.

Cleavage began 40–45 minutes later. The time consumed during the entrance of the spermatozoön, fusion of the pronu-

clei, formation of the amphiaster, etc., is then approximately the same as in *Toxopneustes* eggs fertilized with *Toxopneustes* sperm.

The chromosomes as seen in a polar view of the equatorial plate of $\dfrac{Toxopneustes\ \male}{Toxopneustes\ \female}$ eggs are shown in Figs. 1 and 2.

They are seen to have the appearance of rather long, slender, and somewhat bent rods. By comparing these two figures it may be seen that variations in the form of the chromosomes, which are correlated with slight differences in the ages of the plates, are evident.

A corresponding view of the chromosomes in a section of a $\dfrac{Moira\ \male}{Moira\ \female}$ egg is shown in Fig. 3.

Some differences are apparent, but in general the size, form, etc., of the chromosomes in this plate are so like those of the *Toxopneustes* egg that one need scarcely venture to hope to be able to identify the chromosomes of maternal and paternal origin in the cross-fertilized eggs.

An examination of sections such as are illustrated in Figs. 4 and 5 convinces me that we have here a mixture of the two sorts, but I find myself unwilling or perhaps unable to distinguish the chromosomes of either origin.

Some interesting variations from the normal were found in one series of $\dfrac{Moira\ \male}{Toxopneustes\ \female}$ eggs in which more than one spermatozoön had entered the egg. Two different results are shown in Figs. 9–12 and Text Fig. 1.

In one case the extra sperm-nucleus is seen moving toward the segmentation nucleus. Its aster has divided while the centrosome of the future cleavage amphiaster is still single (Fig. 9). Later the second sperm nucleus seems about to fuse with the segmentation nucleus while the centers of the regular cleavage amphiaster have separated (Fig. 10). In some cases fusion between the two nuclei takes place; in others (Fig. 11), the fibers from one of the sperm asters enter the nucleus and the chromosomes become differentiated in the network before the cleavage asters have well separated.

In the other case (Fig. 12 and Text Fig. 1), chromosomal

differentiation and separation of the cleavage centers had gone on to a considerable extent before the additional spermatozoön had entered the egg. Here the two amphiasters are seen side by side. In Text Fig. 1 what may possibly be sperm tails are seen lying within a fertilization cone, although the entrance of the tail
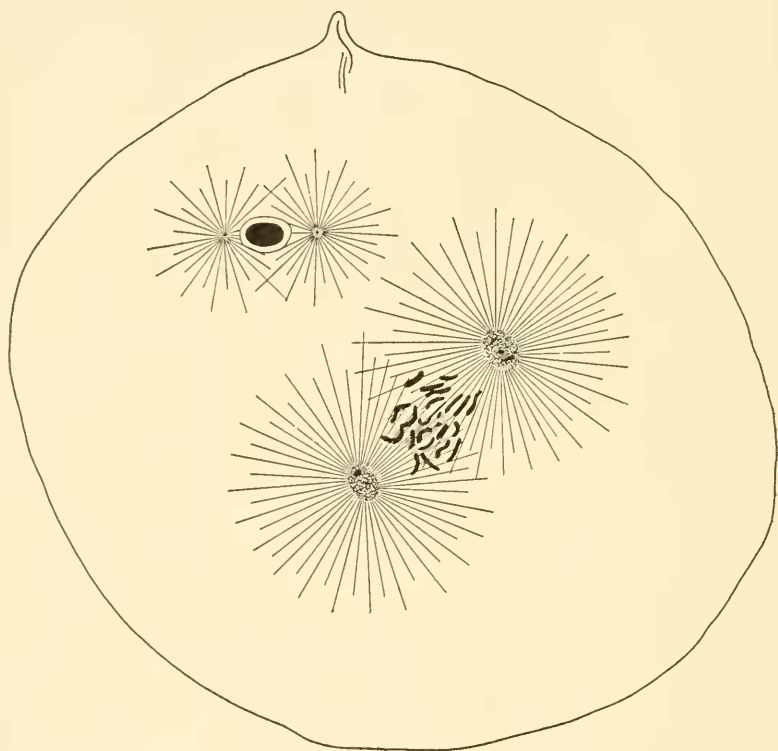
FIG. 1. *Toxopneustes* egg $\times$ *Moira* sperm. (Drawn to same scale and reduced slightly more than are plate figures.) Segmentation nucleus dividing. Extra sperm nucleus in prophase.

in the fertilization of the echinoderm egg is contrary to the general belief.

These cases ought to prove of interest in further investigation along the lines laid down by Boveri in his recent contribution on dispermic sea urchin eggs (Zellen-Studien, Heft 6).

B. The *Moira* ♂ *Arbacia* ♀ Cross.

In effecting this cross the *Arbacia* eggs were allowed to stand in sea water for seven hours, the water being changed every hour, and then fertilized. The controls gave no segmentation.

Cleavage began about forty minutes later ; again approximately as in normally fertilized eggs, in both cases being slightly hastened or retarded by variations in the temperature of the water.

Fig. 2. *Arbacia* egg × *Moira* sperm. Egg outline omitted, otherwise drawn to same scale and reduced as are plate figures. Chromosomes scattered throughout cytoplasm. *Arbacia* chromosomes and *Moira* chromosomes may be distinguished from one another by size.

The sections of eggs of this cross are perhaps of greater interest than those of the *Moira-Toxopneustes* cross because of the fact that the chromosomes of the two species are of sufficient difference in form to be distinguished from one another.

Fig. 6 shows the chromosomes of an equatorial plate of an $\dfrac{Arbacia\ \male}{Arbacia\ \female}$ egg. The chromosomes here are seen to be short, slightly bent rods. These are quite different in form from those already mentioned in the equatorial plate of *Moira* (Fig. 3), where the chromosomes are longer and comparatively more slender.

The sections of the *Moira-Arbacia* cross-fertilized eggs giving a polar view of the equatorial plates (Figs. 7 and 8), show a mixture of short and long forms probably indicating *Arbacia* and *Moira* chromosomes respectively. These differences in form are evident in the equatorial plates of both the first and second cleavages, which is as far as I have carried the observations.

The differences in form are less evident in the late metaphases or early anaphases when the daughter chromosomes are drawn out, behaving like substances with a high surface tension, and then contracting during the late anaphases, into much shorter rods.

In both of the crosses, but especially in sections of eggs of the *Moira-Arbacia* cross, an interesting phenomenon may be noted (Text Fig. 2).

In eggs in which the daughter nuclei are in the resting condition succeeding the first division, the cytoplasm contains many deeply staining rods. The nucleus at this time does not take the chromatin stain and appears like an empty vesicular structure.

In eggs, of the same lot and on the same slides, in which the fibers of the second amphiaster have begun to form, the nucleus again takes the stain and shows the chromatic net, while the cytoplasm is seen to be free from the bodies described.

These structures have puzzled me not a little, but I have finally reached the conclusion that the eggs in which they occur are degenerating. Even though this be true it is difficult to explain the simulation or perhaps occurrence of longitudinal and transverse divisions of these chromosomes lying free in the cytoplasm.

Summary.

This paper deals with observations made on sections of cross-fertilized eggs of two kinds : (1) *Toxopneustes* eggs fertilized with *Moira* sperm, (2) *Arbacia* eggs fertilized with *Moira* sperm.

The results of the study may be summarized as follows :

1. The equatorial plate of the *Moira-Toxopneustes* cross shows a mixture of two kinds of chromosomes not sufficiently unlike one another to enable a positive distinction between the two.

2. The equatorial plate of the *Moira-Arbacia* cross shows a mixture of two kinds of chromosomes, one variety long, the other variety short. These differences in form are correlated with the spermatozoön and the egg respectively.

Bryn Mawr College,
March, 1908.

All of the figures were drawn with the aid of a camera and Zeiss compensation ocular 12 and 2 mm. Apochromatic oil immersion objective. They were enlarged two diameters with a drawing camera and have been reduced to one half in reproduction.

FIG. 1.   *Toxopneustes* egg $\times$ *Toxopneustes* sperm.   Equatorial plate.   Polar view.

FIG. 2.   Same as Fig. 1.

FIG. 3.   *Moira* egg $\times$ *Moira* sperm.   Eq. pl.

FIG. 4.   *Toxopneustes* egg $\times$ *Moira* sperm.   Eq. pl.

FIG. 5.   Same as Fig. 4.

FIG. 6.   *Arbacia* egg $\times$ *Arbacia* sperm.   Eq. pl.

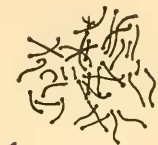FIG. 7.   *Arbacia* egg $\times$ *Moira* sperm.   Eq. pl.

FIG. 8.   Same as Fig. 7.

FIG. 9.   *Toxopneustes* egg $\times$ *Moira* sperm.   Segmentation nucleus with centrosome undivided.   Extra sperm nucleus with aster divided.

FIG. 10.   *Toxopneustes* egg $\times$ *Moira* sperm.   Segmentation nucleus with centrosome divided.   Extra male nucleus, with its aster divided, in contact with segmentation nucleus.

FIG. 11.   *Toxopneustes* egg $\times$ *Moira* sperm.   Segmentation nucleus with centrosome divided.   Fibers from aster of extra sperm nucleus extending into the segmentation nucleus.

FIG. 12.   *Toxopneustes* egg $\times$ *Moira* sperm.   Segmentation nucleus and extra sperm nucleus lying side by side and both preparing for division.
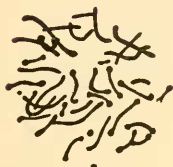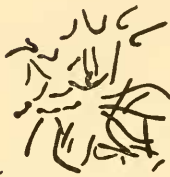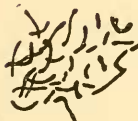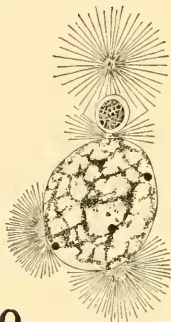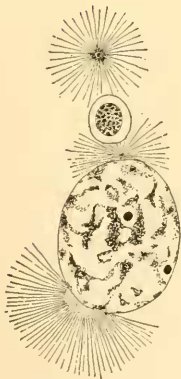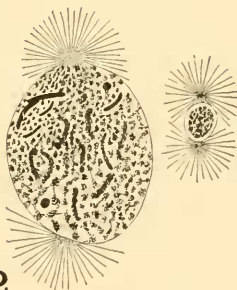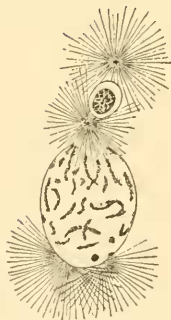
SOME HABITS AND SENSORY ADAPTATIONS OF CAVE–INHABITING BATS.[1]

WALTER LOUIS HAHN.

GENERAL INTRODUCTION.

The present paper embodies the results of about two years of observation on the habits of bats in caves and in the laboratory. The subjects to which special attention has been paid are: The choice of a dwelling; the factors determining times of activity

and rest; feeding habits; breeding habits; and locomotion, including the sense of direction and means of avoiding obstacles. The senses of direction and means of avoiding obstacles have been investigated experimentally. Studies on the other topics have been carried on largely by observation on free and captive animals.

The work was prosecuted from September 20, 1906, to September 7, 1907, while the author held the Speleological Fellowship in Indiana University with residence at the University's Cave Farm three miles east of Mitchell, Indiana. Later the work was continued in the laboratory of the University at Bloomington, Indiana. There are several caves in the vicinity of both places which are inhabited by a large number of bats, thus affording exceptional opportunities for the study.

Some of the notes, especially those on breeding habits, are very brief. However, it is thought best to include them, together with such facts as those contained in the section on morphological peculiarities, in order to give a more complete idea of the biology of the animals. The experimental studies also need to be continued.

The data presented are in part psychological, but it is the purpose of the present paper to treat it from a biological rather than a psychological standpoint.

The work has been carried on under the direction of Dr. C. H. Eigenmann, professor of zoölogy in Indiana University, to whom I am indebted for constant advice and criticism. My thanks are also due to Dr. Charles Zeleny, associate professor of zoölogy, for helpful suggestions and for aid in revising the manuscript.

Previous Work.

Published observations on the habits of North American Bats are limited to scattered paragraphs in natural histories and taxonomic papers. A number of short papers have been published on English, and a few on Continental European bats. The only extensive studies on the subject are two by Rollinat and Trouessart, the first on the reproduction of the Murine (*Vespertilio murinus*) in 1896, and the second on the sense of direction, in 1900.

Morphological Peculiarities and Relationships.

Bats, constituting the order Chiroptera, are more sharply marked off from their nearest relatives than any other group of mammals. Their closest affinities are with the order insectivora which includes such animals as the moles and shrews. However, the separation is a wide one and no known fossils are in any way intermediate between the two orders.

The most important modification is the adaptation to flight. The changes in structure correlated with the habit of aerial locomotion are the following : The fore limb and pectoral bones and muscles are increased in size and the hind limb and pelvis are reduced. The axis of the hind limb is rotated so that the knee projects backward instead of forward. The digits of the fore limb are lengthened to form a support for the wing membrane. A thin, flexible membrane extends from the sides of the body to the tips of the fingers and from in front of the fore arm to the hind limbs and usually includes the space between the latter and the tail.

Other structural peculiarities are as follows : The carpus is reduced or almost wanting. The first digit (thumb) of the manus is short, nearly free from the wing membrane, opposable, and terminated by a curved claw. The other digits of the manus are long, slender, included in the wing membrane and not terminated by nail or claw. The pes has five short, subequal digits, each with a curved claw. The mammæ are pectoral and there is usually but one pair, although a few species have two pairs. The cerebral lobes are without convolutions, and the cerebellum is relatively large. The ear conch has a slender internal lobule called the tragus in most species, and in several families there are foliaceous appendages of skin about the nostrils.

These structural modifications are worthy of note because they are correlated with the characteristic habits of the animals. Walking or running, after the manner of most animals, is seriously impeded by the lengthening of the fingers, the presence of a membrane joining the limbs, and by the reversal of the direction of the knee flexure. Locomotion on solid surfaces is therefore the rare exception and flight is the common method of progression.

The hind limbs are of use chiefly for clinging while at rest ; the fore limbs form only an inadequate support for the animal while at rest and they cannot be used at all for grasping as in most mammals but, as in birds, they are the chief organs of locomotion.

Most insectivorous and carnivorous mammals use the paws to assist in seizing and killing prey and, at times, rest their food against some solid object while eating it. Bats, on the contrary, seize their prey with the mouth, like swallows and flycatchers, and the large, mobile lips assist in holding the food and drawing it into the mouth. They usually masticate it while flying and do not recover any portion that may be dropped.

So greatly has this method of feeding modified the habits of our common vespertilionine bats that the caged animals rarely learn to take food from a dish or from the floor of the cage, although they will eat it readily if it is held directly in front of them.

The expansion of the integument to form the flying membranes has furnished additional surface for bearing organs of special sense and according to Schöbl ('71) a large number of tactile organs are found in the skin of the wing membranes. The nasal appendages and the tragus also have a sensory function, the exact nature of which is not clearly understood.

The nocturnal or crepuscular habit, which is shared by all bats, is doubtless correlated with the increased number of sense organs in the skin which makes the eyes of less importance to the individual and enables it to be active in the absence of light.

Throughout the order there is a relative uniformity of both habit and form. A few species have white markings. In many others the ventral side of the body is paler than the dorsal but otherwise there is a great uniformity of coloration, the prevailing color being some shade of brown. I have seen almost as much variation in the color of a single species from a restricted area as there is in the entire order. While the details of tooth and skeletal structure show that not all the members of the order are closely related, yet the external forms of widely separated groups resemble each other more closely than they do in some of the more nearly related species of other orders.

THE SPECIES STUDIED.

All of the bats found in the United States, except a few species along the southern border, belong to the typical family Vespertilionidæ. In the caves of southern Indiana six species belonging to four genera are found living more or less commonly. In order of greatest abundance they are : The little brown bat, *Myotis lucifugus ;* the Georgian bat, *Pipistrellus subflavus ;* the Say bat, *Myotis subulatus ;* the large brown bat, *Eptesicus fuscus* (*Vespertilio fuscus* of most recent authors) ; the big eared bat, *Corynorhinus macrotis ;* and the large winged bat, *Myotis velifer*. In the literature on the caves of this region, as well as in some of the faunal papers, these species are hopelessly confused· Since the vernacular name, little brown bat, is frequently applied to all of the species except the big eared and large bats, it seems advisable to use the equally convenient scientific names throughout this paper. The observations have been made chiefly on *Myotis lucifugus* but also to a considerable extent on *Myotis subulatus* and *Pipistrellus subflavus*.

These two species of *Myotis* differ chiefly in the size of the ears, the size and shape of the tragus, and some details of cranial structure and dentition. They are about the same size and have the same general appearance and essentially the same habits. *M. lucifugus* is much more abundant than *subulatus*.

Pipistrellus subflavus is much smaller than the other two. It differs from them in color, in the number of the teeth, the form of the skull and other structural details. In habits, it is less active, both in nature and in captivity. For this reason it is not well suited for experiments.

THE PHYSICAL ENVIRONMENT.

All the more detailed observations on bats in a state of nature were made in the caves near Mitchell. Since the conditions there are fairly typical of the natural environment of the animals elsewhere, a somewhat detailed description will be given. The accompanying diagram (Fig. 1) will serve to illustrate the relations of these caverns and openings but not their proportions. The arrows indicate the direction of the stream.

Five caves open on this tract of land, or rather there is a

single chain of subterranean passages with five openings.   These
passages are merely a single underground waterway with a good
sized brook covering the floor in most places.   At two points
the roof has fallen in leaving sections of the stream bed exposed.

FIG. I.   *1*, Entrance to Shawnee Cave ; *2*, lower chamber ; *3*, blind passage ; *4*,
large chamber ; *5*, entrance to Lower Twin Cave ; *6*, entrance to Upper Twin Cave ;
7, entrance to Lower Spring Cave ; *8*, entrance to Upper Spring Cave.   Arrows show
direction of stream.

These openings have been named as separate caves.   The size va-
ries considerably, but the average height is, perhaps, six feet and
the width ten.   In some places it becomes much smaller and the
entire passage is filled with water after a heavy rainfall.   In other
places the size is much greater, in the large chamber (Fig. I, *4*)
the distance from water level to the top of the chamber is about
40 feet and the width at the widest point about 100 feet.   There
are numerous lateral passages varying in width from a few inches
to several feet.   A second large chamber is situated near the
extreme lower end of the cave (Fig. I, *2*).

Temperature records kept for a period of two years, in the
large chamber at *4*, show an extreme variation from about 51°
F. in January, to 57° in September.   The air at this point al-
ways contains moisture nearly to the point of saturation.   Baro-
metic pressure here varies approximately with the surface pres-
sure although the changes take place more slowly.   The physi-
cal environment of the cave-dwelling bats during their periods
of inactivity, is, therefore, nearly constant for all seasons.

Not less than five hundred bats, representing five species, spent
the winter of 1906–7 in these caves.   Probably the number was
much larger, as only those actually seen were counted and some
creep away into the smaller fissures where they cannot be found.
These bats come out of the cave to secure food only in twilight or
darkness in mild weather.

Since the temperature is relatively constant in the cave through-
out the year and there is always total absence of light, the
problem which first presented itself was to determine how the

animals happen to come out at the right time.   For this purpose daily observations were made on the number, location and move- ments of bats in the large room (Fig. 1, *2*) near the Shawnee Cave entrance and also near the entrance of the Twin Cave (Fig. 1, *5*), throughout the year, excepting at several times when the cave stream was too high to permit access to these places.   The large chamber half way between the Shawnee and Twin Cave entrances was visited weekly during most of the year.

Since this work was begun I have visited one or more times about fifteen other caves, ranging in size from unnamed sinkholes to caverns as large as Marengo and Wyandotte in Indiana and Horse and Mammoth Caves in Kentucky.   All of them were inhabited by bats, and in all the approximate number and distribu- tion of these animals have been noted, together with such obser- vations on their habits as it was possible to make.   Live bats have also been under observation in the laboratory from time to time.

Bats have resting places but no homes.   They never construct any sort of a nest or den nor do they habitually return to a fixed spot at regular intervals, although individuals may have a tend- ency to resort frequently to the same place.   Stone and Cram ('02) state that they appear to hang themselves up wherever day- light finds them.   These authors give data which indicate that there may be a periodic return to the same spot at short but irregular intervals.

Of the species found in eastern North Ameria some are habit- ually cave dwellers and some tree dwellers.   The habits of the two groups overlap, however, and at least two of the tree-inhabit- ing species, *Lasiurus cinereus* and *L. borealis* are known to have entered caves in the past.

I have not been able to obtain a reliable record of either of these species living in the caves of the Mississippi valley at the present time.   In the large room (Fig. 1, *4*) of the Shawnee Cave more than two hundred skulls of *L. borealis* and two of *L. cinereus* were found scattered among the rocks on the floor of the chamber.   Careful searching in the same and other places failed to discover the remains of more than twenty-five individuals of the three species now most abundant there.   The skulls, accompanied

by other bones, were scattered among the rocks in a manner indicating that the animals had probably died where they hung suspended from the roof of the cave and that they had not reached the place by accident nor been killed all at one time by a single catastrophe. The age of the remains is difficult to determine. The cave itself is of comparatively recent origin and the bone deposit is evidently much more recent. However, some of the bones must have been there for a considerable period, since they were covered with a deposit of calcium carbonate more than a millimeter in thickness. The remains may indicate that the red bat is a decadent species, represented by fewer individuals at present than in the past, or they may indicate that it has abandoned the cave-dwelling habit in recent times.

During the summer all of the cave-inhabiting species resort to other places, finding temporary homes in attics, deserted buildings, hollow trees and dark nooks in the forest. Merriam ('87) and Miller ('97) have shown that some of the tree-inhabiting species migrate, and there is evidence that *Myotis lucifugus* does also. Just after most of the bats of this species left the Shawnee Cave, about the end of April, 1907, there was a period during which very few were seen flying about in the evening. A few weeks later they were again seen in abundance. It seems probable that the animals which wintered at this place migrated farther north and that the summer residents had passed the winter elsewhere. Howell ('08), describing the diurnal migration of bats near Washington, D. C., states that some of those observed were small and apparently belonged to the genera *Myotis* or *Pipistrellus*. He further states that more than a hundred bats were seen between 9 and 10 a. m. on September 28, 1907. All were flying with the wind in a southwesterly direction, at a height of from 150 to 400 feet. Their manner of flight was unusually steady and consisted chiefly of a sailing or drifting motion with only occasional zigzag movements.

The number and relative abundance of the different species vary without any relation to the size or physical condition of the cave. Mammoth Cave was visited in November, 1907. In a hasty examination of a part of Little Bat Avenue, about 1,000 bats were seen. These were apparently all *M. lucifugus*. The guides

inform me that they are never seen in the inner parts of the cave — probably not more than a mile from the entrance.

Marengo and Wyandotte Caves were visited in July, 1907. Bats never occur in large numbers in the former, perhaps because a building has been erected over the entrance. On the occasion of my visit two were seen, one of them flying, in Mammoth Hall, the other clinging to the wall in the Pillared Palace. In Wyandotte Cave the bats congregate in enormous numbers during the winter. At the time of my visit in summer only a few were seen. Blatchley ('96) states that they reach the innermost recesses of this cave in winter, but gives no localities at which they were seen beyond Crawfish Spring, about two miles from the entrance. The same authority states that he took 401 bats, by actual count, from a space one by one and seven tenths feet square, on a low ceiling in Saltpeter Cave, Crawford County, Indiana.

In the caves of the Donaldson Farm they have been found throughout all of the explored portions, which, in the Upper Spring Cave, extend more than a mile from any known opening. The smaller caves about Bloomington have been visited at intervals throughout the year. In Mayfield's Cave, four and one half miles northwest of Bloomington, the relative abundance of the two most common species is reversed. Banta ('07) states that *P. subflavus* is fairly abundant while *M. lucifugus* was seen only three or four times during three years' observation of the cave. I visited the place January 11, 1907, and December 21 of the same year, and confirmed his observations, finding 17 of the first species and 2 of the second on my first visit and 22 and 3 respectively at the second visit.

P. subflavus was more abundant also in Strong's Cave one mile from Mayfield's, during the winter of 1907–8. In Truitt's Cave, 2¾ miles from Mayfield's, and considerably larger, there were 40 *P. subflavus* and 51 *M. lucifugus* on November 29, 1907. In Coon Cave, 2 miles from Truitt's and 4½ from Mayfield's, there were about 500 bats on March 29, 1908, not more than 50 of which were *P. subflavus*. Two *M. subulatus* were seen and a few others may have been overlooked; the others were *M. lucifugus*. Eller's Cave, visited on the same day as Coon, was inhabited by about 100 bats. Approximately nine tenths of them were *M. lucifugus* and the remainder *P. subflavus*.

Both of these common species have been seen in some very small caves near Mitchell. In one of these, at least, they seem to have wintered, as several were found there on March 26, and a single *Pipistrellus* was seen under a ledge of rock just outside the entrance in February. This cave is merely an irregularly spiral sink-hole going down to a depth of forty feet but without any large lateral passages. All parts of it receive daylight on bright days and the temperature certainly falls quite low in cold weather.

The other caves mentioned vary in size from the two largest known caverns in North America to small caves with not more than half a mile of passages that are large enough to be explored. The entrance to some of them is a vertical shaft, to others it is a horizontal passage going into the side of a hill.

The conditions prevailing within a cave do not determine a bat's choice of a resting place after it has entered. In Coon Cave, as well as several others that I have visited, there is running water at one point and the air here is usually saturated with moisture. In the upper part of the cave, some distance from the entrance, the atmosphere is always dry and the floor and walls dusty. When I visited this cave, bats were about equally abundant in the dry and in the wet parts. In the latter places the moisture had condensed on the animals and drops of water hung from their fur. The arrangement of hairs is such that this moisture does not penetrate to the skin unless the animal is rubbed in moving about.

Usually the animals go far enough into the cave to be in total darkness and a nearly constant temperature, although as mentioned later (p. 163), they sometimes remain for several weeks where they are reached by both light and cold. Blatchley states that "bats choose as a resting place that part of the roof where small portions have begun to flake, giving a certain degree of roughness, or small crevices, to which they can cling. They cannot attach their claws to a smooth surface, hence from large portions of the roof of a room they may be entirely absent." This statement is partly erroneous, for although they cannot attach their claws to a polished surface, the limestone walls and roof of a cave are ordinarily rough enough to furnish adequate support.

I have frequently found colonies clinging to the roof in places where there were no large prominences and no crevices, and I have seen flying bats secure a foothold in such places in the cave, and also to smooth, but unplaned, lumber in a house. The top and side walls are preferred equally by the different species of *Myotis*, but *Pipistrellus* is generally found on the side walls of the higher chambers. The claws of both feet are hooked about prominences on the stone and when the animal is resting on a vertical wall, the wrist and the nails of the thumbs also rest against the wall and form some support. However, the feet alone are strong enough to support the animal for weeks at a time and even to support several others of its kind when they cling to it.

The social habit is strongly developed in *M. lucifugus*. The large colonies seen by Blatchley in Wyandotte and Saltpeter Caves were almost certainly of this species, although he calls them *M. subulatus*. I have never seen them hanging in clusters as large as these but have frequently seen bunches of fifty or more. The guides at the former of these caves tell me that bats gather there in winter in clusters comparable only to a swarm of bees, and probably equalling such a swarm in number of individuals. *Myotis subulatus* and *M. velifer* are not abundant in this region but are generally found associated with groups of their abundant congener.

Corynorhinus macrotis has only been seen in dim light near the entrances, and there it was found clinging to the side walls with its long ears folded down along the sides of the neck. *Eptesicus fuscus* has not been seen far within the caves nor is it abundant. The largest number I have found in one place is six, taken near the entrance of Mayfield's cave on December 21.

Pipistrellus subflavus is solitary in habit. Occasionally two are found side by side, though I have never seen them clinging to each other except in mating. However, they do not avoid the vicinity of others of their own kind nor other species. This species seems to prefer the side walls of the higher passages. I have never seen it suspended from the roof except where there was a crevice or prominent ledge.

ENEMIES.

Very few enemies molest bats in their roosting places in the caves. In Eller's Cave I saw evidence that raccoons had been preying on them. It is said that cats have learned to catch the flying bats in Wyandotte Cave. No doubt other carnivora sometimes kill them, but on the whole they are practically free from molestation in the caves. While living in trees they are doubtless preyed upon more frequently. In two instances I have known them to be driven from their roost by birds, once by a robin and once by a blue jay. The barn and great horned owls and the sparrow-hawk have been known to eat them in rare instances.

Their enemies are so few, however, that they have no sense of fear comparable to that of other small mammals. A sharp noise will sometimes startle them into activity. If wide awake they may fly before they can be picked up by hand or net, or if caught they often struggle to get free. But there is never any attempt to "lay low" or to flee from approaching danger. When kept in cages they do not pay the slightest attention to the presence of man, nor try to escape his hand if he attempts to pick them up, even when first brought into captivity. The absence of fear has a marked effect upon the habits and mental life of the animals. Only in such species as are without natural enemies is it possible that there can be such long periods of inactivity or such a deep lethargy in normal sleep.

PERIODS OF ACTIVITY AND REST.

Bats are usually active only in the twilight and darkness during warm or moderate weather. The earliest date at which I have seen them flying at a distance from their dwelling place was March 3, 1906, at Washington, D. C. The evening was balmy but there was snow on the ground in places. The latest date I have seen them was November 8, 1906. The evening was warm but had been preceded by some hard frosts. I have seen them come to the mouth of a cave in midwinter and turn back when they felt the cold air. On warm winter nights they no doubt prolong these excursions.

Since they live a part of the time in the caves where there is a total absence of light and where the temperature varies only a few degrees throughout the year, the question has been asked, how do they know when to come out (Blatchley, '96)? The answer is, they try conditions and only come out under favorable circumstances. So far as I know, careful observations bearing on this point have not hitherto been made and it seems worth while to record my own in some detail.

In the first place, hibernation among bats is not strictly comparable to the same process among the lower vertebrates, since it is not one unbroken period of torpor more or less dependent on temperature (Oldham, '05 ; Rollinat and Trouessart, '96). The vital functions of a frog may be practically suspended during a long period, the lungs and digestive organs almost ceasing to function for the entire winter. In bats the activity of the vital organs decreases, though only to a limited degree. The rate of respiration is difficult to count accurately because the body movement is slight. I have counted the respiration of a dormant bat in the cave at several times during the winter and found the rate to be about 60. At other times I have seen the animals apparently cease to breathe for periods as long as four and a half minutes, and then after one or two convulsive respirations, the frequency would suddenly go up to as high as 82 per minute. I am not certain that breathing actually ceased during the quiescent period but there was no visible body movement. In any case, the same conditions are found during profound diurnal sleep at all seasons of the year.

The animals do not obtain food during the winter but the stored fat is used up and wastes are excreted from the body. Oldham ('05) found fecal matter in the intestine of the lesser horseshoe bat (*Rhinolophus hipposideros*) during the winter and regarded it as proof that the animals had been eating recently. However, fecal matter is, in part, derived from wastes excreted through the wall of the lower part of intestine and is not dependent upon food. The presence of feces is, therefore, no indication that an animal has recently eaten. Lusk[1] states that a fast-

[1] "Science of Nutrition," Graham Lusk, p. 46.

ing dog weighing 30 kilograms excreted 1.88 grams of fecal matter per day.   In the large number of bats which I have dissected in winter, the stomach and upper part of the intestine was always empty, although feces were present in the rectum.   I am convinced that the cave bats of southern Indiana seldom or never eat during the winter, the stored fat being sufficient to sustain life.

The degree of lethargy bears a close relation to the quantity of superficial fat stored up by the animal and it is not related to the temperature, either without or within the cave, nor to season. In fact, the period of least activity is in the autumn and early winter, before severe weather has begun.   The bats are often quite active in the cave during the cold weather of late winter. Between August 8 and September 5, 1907, I took a number of bats, *Pipistrellus subflavus*, *Myotis lucifugus*, and *M. subulatus* from the caves to use in experiments.   Some of these were very fat while others were comparatively poor.   On September 5 I used two males of *P. subflavus*.   The first one was quite poor and flew readily when released in the room after being carried for a short distance in a small box.   The second bat had to be prodded and tossed about before it could be awakened from its lethargy sufficiently to fly.   Even then its movements were more sluggish and it struck obstacles oftener and also had to be frequently disturbed in order to keep it in motion.   I have never seen a bat more difficult to arouse at any time during the winter nor one more torpid when once induced to fly.   An examination showed that this animal was exceedingly fat.   This is not an isolated case but merely illustrates what has been found several times in this and other species.

When in a state of lethargy, a bat cannot be quickly aroused. Neither noise nor light appears to be a sufficient stimulus to awaken it.   Heat will arouse it more quickly than any other stimulus and it will immediately draw away from the heat of a candle.   Mechanical stimuli are also effective and bats are sometimes aroused from torpor by being carried for a distance.   Merzbacher ('03) found that the reactions of hibernating bats are similar to those in which the cerebral hemispheres have been destroyed.   The clinging reflex is very evident, even in the most torpid animals.   In the torpid state the body temperature falls

to such an extent that the limbs and membranes feel cold to the touch. As the animals are aroused, the breathing becomes stronger, the temperature rises, the eyes open and often there are convulsive movements of the limbs. The animal may also begin to chatter and to creep slowly. If laid on its back it slowly rights itself. However, it is some time before it gains full control over its muscles. If dropped, the wings spread reflexly, but the animal cannot at once fly. There are intermediate stages of lethargy in which the torpor is less extreme and the animal very quickly gains power over its body, but the extreme conditions described above have been observed in every month of the year except May, June and July, during which months but few bats have been under observation.

Observations on periodic movements of bats were made chiefly at two points in the caves at Mitchell, in the large chamber (Fig. 1, 2) at the right of Shawnee Cave, and at a point about 100 feet within the Twin Cave entrance (5). Both points are so near the entrance that the temperature varies considerably. On bright days a diffuse light reaches both points for an hour or more when the sun's rays fall directly into the mouth of the cave. Daily observations were recorded from January to April, 1907, with the exception of several times when high water prevented entering the cave.

On January 2, with a maximum temperature of 50° F., there were 75 bats at the place of observation in the Twin Cave. A period of low temperature followed, and high water prevented further observations until January 25, when the number had decreased to 9. The number now increased gradually until February 7, when there were 51, although the temperature remained low. With the average temperature slightly rising, the number of bats diminished during the next two weeks to 42 on the twenty-first of the same month. During the next four weeks the number of bats again increased until on March 20 there were 101. The temperature had been rising gradually and with some fluctuations, and the average daily temperature on March 20 was about 45°; a further rise to 70° on March 27 followed. With these higher temperatures the number of bats on the twenty-eighth of that month was only 18. Unseasonably

cold weather during April was accompanied by an increase in
bats which reached a maximum of 153 on April 20. Observa-
tions carried on during the same period at 2 (Fig. 1), which is
another part of the same cavern, showed a variation in the num-
ber of bats near the entrance which almost exactly paralleled
that in Twin Cave, thus showing that the movements had some
common cause and were not wholly accidental.

Apparently the movements have a definite relation to season
and temperature. The bats come to the mouth of the cave at in-
tervals throughout the winter, but these intervals are longer in
the early winter when the animals are fat and well nourished.
The unusually warm weather prevailing early in January may
have acted as a stimulus for them to remain near the entrance ;
no doubt some individuals left the cave at night in search of food.
Cold weather followed and the cold, entering the cave, drove the
animals back to the warmer parts. However the hunger stimulus
was becoming stronger and the bats came to the entrance more
frequently and tended to remain there. The maximum number
was reached with a moderate temperature, and when the weather
became quite warm the animals left the cave and did not all re-
turn but found temporary homes in trees and buildings. Cold
weather in April brought them back to the cave again, but most
of them remained near the entrance. When the weather again
became warm at the end of April, they left the cave for the
summer.

Other observations were made on the movements of individual
bats at different times. The location and orientation of different
individuals were carefully marked and the place was visited
weekly. Out of 18 bats observed between November 19 and
December 3, 14 had moved within one week, and none remained
in the same place during two weeks. Later in the winter one bat
remained in the same spot near the entrance from February 4 to
27. Light reached the spot throughout the day and the tem-
perature remained near freezing point for several days at a time.
However, this was an exceptional case, as not many bats remained
in one location for more than four or five days during the latter
part of the winter. The small bat, *P. subflavus*, is less active.
Its average period of staying in one place is about two weeks,
and one was noted in the same spot for 44 days.

Data on the daily movements of bats are still very meager. Moffat ('05), who has observed Irish bats, states that among the Irish bats, Daubenton's, the pipistrelle, and the long-eared fly all night. The Noctule flies in the evening twilight, and the hairy-armed flies for about an hour shortly after sunset, then retires to its roost and again comes out shortly before sunrise. Six pipistrelles, living solitary, were found to have similar, and very regular habits, leaving the holes in hollow trees from ten to thirty minutes after sunset, and returning from forty to eighteen minutes before sunrise. The observations, which were made in August, showed that there was no difference for warm nights and raw, cool nights. Morao ('63) states that the bats in an immense colony of *Myotis lucifugus* in the attic of a house near Charlestown, Maryland, were accustomed to leave their roost twice in one night. His somewhat poetic statement that they left at "the call of the whip-poor-will" cannot be considered accurate, for in such a large colony, individuals could not be noted and any general disturbance of the colony might be mistaken for a renewal of the activity of the individuals.

The same difficulty exists with regard to determining the daily activity of bats in a cave. Their dwelling place is so large, and the possible exits usually more than one, so that their movements cannot be watched. It is possible to go into the cave and examine individuals, but there is the danger of disturbing them and causing them to leave sooner than they would if unmolested.

I have seen bats flying in the cave at all hours of the day and night, and have also found them at rest there at all hours. Evidently they may awaken from sleep at any time and fly to the mouth of the cave. If the temperature and light are favorable they go out and search for food. If it is cold or if the light is too strong, they go back. If they are fat and well nourished they settle down to another more or less prolonged period of lethargy. But if the hunger is strong they are apt to remain awake and active, or only go to sleep for a short time.

The bats in the clusters seen in spring or late winter were usually awake and chattering. In the fall and early winter bats are generally isolated and torpid. Those that are active are very apt to reach the mouth of the cave as soon as conditions out of

doors are favorable for their activities. The presence of bats in the cave at night, when others are out searching for food, shows that there is no definite time at which they all leave their roosts. This fact has also been observed with regard to the European pipistrelle (*Pipistrellus pipistrellus*) by Whitaker ('07), who says that only part of a large colony left their roost under a roof on a certain night. If a large percentage of the animals does become active at about the same time, it must be remembered that many of them pass the summer in places where daylight reaches them and the absence of light as night falls may be a direct stimulus to activity. Falling temperature at sunset may also stimulate the animals to activity when they are not in the caves.

On rare occasions the hunger stimulus may be so strong as to overcome the natural repugnance to light, and the animals come out to search for food in daylight. I have witnessed this but twice. In late autumn a *Pipistrellus* was seen circling high above the trees, and at another time, May 9, 1907, a *Myotis lucifugus* was seen feeding in the bright noonday sun near the mouth of Shawnee Cave.

On the average, a bat certainly does not fly more than six hours out of twenty-four, and that for not more than eight months of the year. At least five sixths of its life is spent hanging head downward in the dark.

From the foregoing facts we may assume that a bat's life is made up of a series of alternating periods of torpor and activity. The relative and absolute length of these periods depends on the state of bodily nutrition.[1] When the body is well nourished and the quantity of reserve fat large, the periods of lethargy are long and the time of activity short. As the stored fat is used up the periods of lethargy become shorter and active states longer and more frequent. During the season of greatest activity, from May to July inclusive, the times may correspond to daylight and darkness, and the condition of the animals to ordinary sleep and activity. However, the longer periods have no direct relation to

[1] The physiology of hibernating bats has been studied by Rulot ('02) and Merzbacher ('03). According to the former, glycogen and albumen are consumed during hibernation, especially toward the end of the period. It is evident that the hibernating state in the bats studied by these authors is more profound than it is in the bats which I obtained in the caves.

season or temperature nor are any of the periods dependent upon the physical environment.

Feeding Habits and the Perception of Food.

The feeding habits of bats are by no means easy to study. They habitually secure their food while flying, and then only during twilight or darkness when it is impossible to distinguish their movements accurately. In a state of nature their food consists largely, perhaps wholly, of insects. The single time that I have seen a bat feeding in daylight near enough to distinguish its prey, it was catching small ephermerids and diptera. At dusk they can sometimes be seen pursuing larger insects, apparently beetles. The food is so thoroughly masticated that examination of stomach contents furnishes no definite clue to the identity of the things eaten. Neither does the food that an animal will eat in captivity afford an index to its natural food. Meal worms seem to be the favorite article of diet of captive bats. Fresh meat is eaten readily. They will also eat a small worm (*Tubifex*) which lives only in mud and certainly is never eaten by the animals in nature and has not been by their ancestors since the flying habit was acquired.

Dobson ('78) states that a fruit bat (*Cynopterus*) which he captured in Calcutta consumed a banana twice its own weight in three hours. Whitaker [1] states that the hairy armed bat, *Ptergystes leisleri*, eats about five dozen meal worms a day, and that a female noctule, *P. noctula* [2] after several days fasting, during which she gave birth to young, consumed eight dozen meal worms in one evening. None of the bats which I have had in captivity have been voracious eaters. Captive bats will learn to eat meal worms greedily when they are offered to the animal with the fingers or a pair of forceps. Only on one or two occasions have I ever seen a bat pick up food from the floor. When a meal worm is taken between a pair of forceps and held before a bat, the animal will snap at it eagerly, especially if the worm is wriggling. However, its efforts are not well directed and it is as apt to get the forceps in its mouth, or to miss the objects completely, as it is to seize the worm.

When food is accidently dropped the bat does not make any

[1] '07.   [2] '05.

attempt to recover it and does not even turn its head to look for the lost morsel ; generations of flying ancestors have not found it advantageous to try to recover an object dropped while on the wing.

Bats are not wholly dependent on a single sense for distinguishing their food.   Smell, on which many other mammals are chiefly dependent, here is of subordinate importance.   The reason is to be found in the way in which food is secured.   Any creature walking on a solid surface and having a characteristic odor, can be located, or can be traced some time later, by an animal with a keen sense of smell.   But flying insects, which form the chief food of bats, do not leave a permanent odor in their path nor can their presence be definitely localized because the odors are diffused too rapidly and unevenly by shifting currents of air.   I have held meat, meal worms and insects near a hungry bat and it did not seem to notice their presence until some sense besides smell was stimulated.   However, fresh meat fastened to the side of the cage was found and eaten after a time.   On one occasion a bat that was running across the floor of a cage perceived a piece of meal worm it was passing and picked it up.   This was, however, the only instance of the sort I have observed in handling and feeding a large number of bats.   The same animal and others seemed quite unable to find meal worms or insects lying quietly on the bottom of the cage.   Occasionally they found meat placed in a small dish.   This happened more often with *Eptesicus* and *Pipistrellus* than with either species of *Myotis*, though the latter found the meat more readily when it was fastened to the side of the cage so that the animals climbed about over it.

It must not be inferred from the above statements that the sense of smell is lacking, or even rudimentary.   All bats have a strong odor, the purpose of which is probably to attract others of their kind.   This may be taken as an indication that smell is well developed, for otherwise the odor would be useless.   The action of the animal mentioned above in stopping to pick up the meal worm, and the ease with which others learned to find and eat such unfamiliar food as meat, also indicate that the sense of smell is not lacking.   The fact that they do not usually notice food when it could be perceived by this sense alone, indicates only that they are not accustomed to find it in that way.

After extended observations on the subject, I am still unable to form any definite conclusions with regard to the importance of sight to these animals. That they can see light and darkness and moving objects is unquestionable. That the sense of sight is not highly developed is equally certain. The behavior of some of the animals appears to indicate that at times they depend on this sense to a considerable degree, both in securing food and in avoiding objects.

On bright nights, and in twilight, a dark, moving object can be readily seen against the skyline. Under such circumstances sight would be of use to bats in helping them to find the general location of food. Whether it really guides them at such times is a point not yet determined.

Bats are extremely sensitive to vibrations of high frequency. A sharp whistle, sucking noises with the lips, tearing a sheet of paper and drawing the finger nail across a piece of thin board or rough cardboard cause them to start violently, but low pitched, rumbling noises have no apparent effect.

Flying insects usually produce a high-pitched hum. While it would be of advantage to a bat to perceive these sounds, the evidence that they are actually guided to their prey by hearing them is inconclusive. It is not possible in observations on feeding to distinguish between response to hearing and to tactile stimulation, by the vibrations. The voice of different species of bats varies but it is always high pitched. Alcock ('99) states that the voice of the hairy-armed bat has about 17,000 vibrations per second. The pitch has not been determined for the voice of the American species.

It is evident, however, that it is the *motion* of the insects that lead to their perception by bats. Whitaker ('06) states that a noctule which he observed caught a pebble tossed into the air. In this country boys often gather under the electric lights or at the edge of a wood where bats are abundant in the evening, and knock them down with a fishing pole waved rapidly in the air. In both cases the bats are attracted by the moving object and probably by hearing. The tactile sense, located in the vibrissæ and lips, is certainly very delicate and doubtless aids the animal to definitely locate its food. In feeding meal worms to bats I

have found that the animals do not, as a rule, pay any attention
to worms held near them so long as they are quiet. But when
the worms begin to wriggle the bats at once become excited and
begin to snap at them. This happens when they are not touched
by the worms and when the latter are out of the range of vision.
It seems improbable that touch is the sense here aroused. The
food must have been perceived by the tactile organs being stimu-
lated by air currents set in motion by the moving worms.

It is said that bats use the interfemoral membrane, which the
flying animal carries curved downward and forward under the
body, as a sort of scoop in which insects are caught. It is pos-
sible that food is thus secured at times, but it is more often seized
in the mouth. However, the membrane is used as a pouch into
which the bat thrusts its head when it has an insecure hold on
an insect. The membrane thus serves as a pouch to prevent
dropping the food and also serves as an object against which the
struggling prey can be pressed while a firmer hold is being
secured.

Observers (Whitaker, '06 ; Grabham, '99), who have studied
the habits of various European species of bats agree that they
drink while on the wing, flying over a body of water and dipping
down to its surface to drink. I have observed the same habit in
M. lucifugus ; it probably alights to drink also. When in cap-
tivity this species learns readily to come to a small cup of water
placed on the floor of its cage. The animal gets up on the edge
of the dish, resting on its wings and body and bracing with its
feet. Often it dips a part of the forearm and wing into the water.
The lower jaw and tongue are thrust in, the mouth is filled with
water and, generally, but not always, the head is raised to its
normal position and the water is taken down in a succession of
rapid swallows. On the whole, the method of drinking resembles
that of a young chick, except that the head is not lifted so high.

If the conclusions given above as to the manner of perceiving
food are correct, it is obvious that water must be perceived in some
other way, since it is obtained where it is relatively stationary and
noiseless. On two occasions I have seen bats in the laboratory
apparently attempt to drink while flying. On the first occasion
there was an aquarium of running water in the room. The bat

flew near enough to this to feel the splashing water and then turned and flew repeatedly across the room, keeping near the floor and frequently giving the floor an audible bump with its opened lower jaw. The other time there was no running water in the room which could have set off the impulse, but there was standing water which it may or may not have approached. On both occasions there was a good light, either artificial or daylight, and the floor was of a dull, yellowish brown color which might look to an animal flying over it like water of a pond on a starlit night.

The evidence at hand is not sufficient to prove the point, but it seems probable that sight may be the sense by which water is usually distinguished, but that moisture-laden air, rising from a body of water to a bat flying above it, also helps the animal to locate water.

I am unable to say whether bats ever drink in the caves. In most places there is so much moisture that they probably do not become thirsty. There is no evidence to show that they ever eat in the caves. Some insects could be obtained there but the quantity would be inconsequential as compared with the number of bats to eat them. The lack of sufficient food is doubtless the only reason that they have never become true cave dwellers.

Locomotion.

Bats are more helpless on their feet than most birds. This is in part due to the mechanical impediment of the flying membrane, and in part to the skeletal modification outlined in the section on morphological characters. As a result of these changes in form the animals cannot support themselves on their hind limbs alone, as do birds and man, nor can they rest upon the terminal part of the fore limbs. When walking upon a horizontal surface a bat rests upon the sole and claws of the hind foot and upon the carpus and thumb of the fore limb. The phalanges are usually folded backward along the fore arm, as when at rest, though the wing is sometimes slightly expanded. The tail and interfemoral membrane are curved forward under the body and both the tail and the wing may touch the floor at times. The body is elevated so that it clears the floor. The limbs are moved as in other

mammals, the right hind limb being lifted with the left fore limb, and vice versa. The steps are necessarily very short because the membranes prevent long steps, although they are sometimes quiet rapid. This rapid movement across the floor has been very well described as "scurrying." It is never kept up for a long distance. The animals apparently become tired in a run of a few yards.

Flying is the usual mode of locomotion for bats and they have the capacity for flight developed to a high degree. We have no definite information as to the speed of a flying bat, the duration of its periods of flight, nor the distance that it will travel from either its birthplace or its temporary dwelling. Some of the animals that I have had in captivity seemed to tire very quickly and could not be easily induced to take to flight when they had once settled down. Attempts to estimate their speed can be scarcely more than a guess because their erratic, wavering flight is much more difficult to measure than that of a bird, and because of their nocturnal habits. *Myotis lucifugus* probably flies at a rate of about ten to twelve miles an hour. *E. fuscus* flies faster and *P. subflavus* not so fast. The flight of the last named species is weak and wavering and resembles that of a butterfly. *E. fuscus* has a relatively rapid, strong and steady flight, while *Myotis lucifugus* and *M. subulatus* are, in a way, intermediate between the two.

The quick turns and evolutions which bats make as they fly about in the twilight are for the purpose of catching flying insects. However, their manner of flight is essentially the same when they are not feeding. It may be that this erratic flight has some relation to the kind of place in which these animals are accustomed to live. In the earlier stages of the evolution of flight, bats must have lived in trees and their movements must have consisted of short leaps or flights among the branches, where skill in avoiding the limbs and in clinging to them was of more consequence than steady or prolonged flight. As the power of flight became better perfected the animals would still secure their food largely among the trees, but would remain on the wing longer and would dart here and there among the branches snatching food as they went. Hence the importance of being able to readily perceive and avoid small objects. The cave-dwelling habit would tend to further develop

these peculiarities, since the angles and projecting ledges of the caves would prevent a straight and continuous flight. Catching insects on the wing would make agility count for more than endurance and steadiness, and hence the characteristic mode of flight has been preserved.

The migrations previously mentioned (p. 155) would seem to indicate that individuals may travel five or six hundred miles twice a year. The steady flight noticed by Howell ('08) in diurnal migration may be taken as an indication that these animals make long, continuous flights and have considerable endurance. In this characteristic we find another analogy to birds.

A flying bat can change its course or check its momentum very quickly. When it does not perceive a solid object that it is approaching, it sometimes strikes its head while going full tilt and falls down. Usually, however, an object is perceived before actual contact takes place, and in that case the animal is always able to check its flight and alight on the obstacle if it is too near to turn aside and avoid it.

The quick turns and dodges seem to be made by changing the angle of the wings either antero-posteriorly or dorso-ventrally. The interfemoral membrane and tail may act as a rudder, but a bat from which they had been removed flew as well as before the operation.

A flying bat can alight on a vertical wall in several different positions. Oldham ('05) states that the British Vespertilionidæ alight on vertical surfaces with the head upward and reverse quickly after obtaining a foothold, while the lesser horseshoe bat (family Rhinolophidæ) reverses in the air and alights head downward. Both of our common species of *Myotis*, and I think all of our other cave-inhabiting bats, can reverse in the air and alight head downward although they do not always do so. When flying against a window screen or some other object, not perceived until it is almost touched, they alight head up, striking with the anterior end of the body first and letting the posterior end settle down.

The reversal consists in a sidewise dip with wing and head, the hind limbs being brought forward and thrown upward at the

same time so that the one wing is directly above the other ; the sidewise motion then continues far enough to bring the head under the tail and the claws of the feet grasp the surface.   If the wall is too smooth to furnish a foothold the bat is in position for immediate flight.   Sometimes   the   position   is   only   partially reversed and the animal alights sidewise.   In this case the thumbs support most of the weight.

A flying bat can secure a foothold upon a horizontal surface beneath which it is flying as easily as on a vertical wall.   To secure a foothold the bat throws its head downward and its feet upward and forward till they touch the roof and the claws grasp the supporting object.   The quickness with which the momentum of flight is checked is one of the nicest adaptations of a bat's life.   Only a slight roughness is necessary for the sharp curved claws to secure a firm hold.   I have seen a flying bat clasp and hold a vertical number 16 wire that it accidentally struck.   The fore arms were placed behind the wire which was pressed against the back as a man might hold a cane thrown across his shoulders. A bat in flight can catch a rafter or similar object by a single thumb, or by the claws of one foot.   Metal, glass, polished wood or stone are not rough enough to furnish support, but unplaned boards, and rough limestone, furnish adequate foothold.

When a bat launches into flight from a perch on the roof or side wall, it always drops downward, spreading the wings as it drops.   It can launch into flight from the floor or other flat surface, but it cannot rise vertically in the air from a resting position. A bat which fell into an empty aquarium, 16 inches in diameter, and the same depth, was unable either to climb its smooth sides or to fly out of it.   When caught in a dip net they are unable to fly out of it, but must climb the sides and fly from the rim to escape, a fact which makes it easier to capture them.

Breeding Habits.

The reproduction of some of the European bats belonging to the families Rhinolophidæ and Vespertilionidæ has been studied by several zoölogists.   Benecke ('79), Eimer ('79), Van Beneden and Rollinat and Trouessart ('96), all state that copulation takes place in late summer or autumn.   The spermatozoa fill the lu-

men of the uterus and remain alive but inactive throughout the winter. Ovulation and fertilization take place at the return to active life in the spring and development begins at once and continues without a resting stage. Duval ('95) states that bats copulate a second time immediately after hibernation, but Rollinat and Trouessart ('96, p. 220) consider his observations to be erroneous.

The reproduction of American bats has not been studied in detail. I found *Myotis lucifugus* copulating in Shawnee Cave on October 27, 1906, and at two unrecorded dates shortly afterward. In Truitt's cave I saw a pair copulating on October 19, 1907. Two pairs of *Pipistrellus* were apparently copulating in the same cave on November 29, but they were too high to be reached and I could not be certain. A pair of *Myotis subulatus* appeared to be copulating early in April, 1907, but they also were in a position where they could not be obtained or be carefully watched. If mating actually took place at this time it may have been the post-hibernal mating mentioned by Duval, as it is extremely improbable that this species would copulate at a very different season from its near relative.

In sexual congress the female clings to a vertical wall or ledge. The male attaches himself to the posterior part of the body of his mate, and clings to her fur and membranes with his claws, but also rests in part on the interfemoral membrane and body. The posterior portion of his body is flexed forward, pushing aside the interfemoral membrane of the female, so that contact between the genital organs can take place. Coues and Yarrow ('75) state that the red bat (*Lasiurus borealis*) copulates during flight, but this statement is so at variance with the facts observed for the other species that it cannot be accepted without further confirmation.

The uterine contents of *M. lucifugus* were not examined to determine at what time fertilization takes place. However, embryos were not present in any that have been examined in the caves, including several as late as April 9, and one on April 27. It can be asserted, that in this species, development does not begin until the beginning of the summer activity of the female. After this time the females seldom or never enter the caves and I have

not been able to find them at all during the period of gestation and the rearing of the young, nor have I ever found the young bats of either species of *Myotis* before they had reached adult size.

Pipistrellus likewise leaves the cave for the breeding season, although I have taken a female of this species containing three small (about 2 mm.) embryos in the Twin Cave on June 6.

The males of certain oriental species of bats (*Chiromeles torquatus* and some of the species of *Cynopterus*) have special adaptations for carrying the young. The Standard Natural History (p. 161) generalizes from this fact so far as to say that "it is not doubtful that the male attends to his mate and young with considerable assiduity." The absurdity of this statement in so far as it applies to our common Vespertilionidæ, is apparent from the further statement on the same page that "the sexes do not mingle and come together only at the nuptial season." There is almost certainly no permanent mating but the animals copulate indiscriminately, several males perhaps mating with one female. This is what might be expected in gregarious animals that do not rear their young in a nest or den, but give birth to them at any convenient place and carry them about. Rollinat and Trouessart ('96) believe that this is what happens in the case of *Pipistrellus pipistrellus* and *Vespertilio murinus*.

The females of our species of *Myotis*, and perhaps the other Vespertilionidæ of eastern America, probably seek out isolated places in which they give birth to the young and where they spend most of the time while rearing them. As long as they remain in the cave in the spring there is no complete segregation of the sexes. I have found the two sexes associated in Twin Cave on different dates in April (the latest examination was made on April 25) both in the years 1907 and 1908.

The females leave the caves somewhat earlier than the males. On April 25, 1908, in a search through the outer parts of all the caves on the Cave Farm, I found 23 male *P. subflavus* and 4 females. Twenty-five male *M. lucifugus* were also found, to only 2 females of that species. On May 13, in Truitt's Cave, there were 17 *P. subflavus* and 5 *M. lucifugus*, all of both species being males.

The Behavior of Bats in Captivity.

Bats in captivity, as well as those at liberty, are very erratic and uncertain in their behavior. Some of them are sluggish and cannot be used at all for experimentation. Others are quite active for a time and then suddenly retire to some corner, hang themselves up by the feet, and do not move from their chosen position for hours, or even days, unless they are disturbed. If disturbed, they sometimes open their mouths and chatter angrily, but do not move unless forcibly pushed aside. Others will fly a short distance and then settle down again. Occasionally a repeated disturbance will arouse them to complete activity.

They learn to go and drink from a small dish of water placed in their cage. Some have learned to go to a dish of raw meat and eat. As a rule, however, they do not find food on the floor of the cage, but will eat more readily if meat is placed on the sides, where their head comes in close contact with it as they move about.

Insects are not readily eaten unless presented to them with fingers or forceps. Meal-worms are eaten with much apparent relish, but often, especially in winter, even this food has to be thrust into their mouths so that they will taste it before they learn to eat. I have often turned the meal-worms loose in a cage or small box with bats, but not one has ever been picked up as it was crawling around, although they sometimes crawl over the animal's body and membranes.

The manner of eating, and the time required for the consumption of the same amount of food, varies considerably at different times and with different individuals. They eat slowly as compared with other animals of equal size ; from one to five minutes being required for eating a single meal-worm. Some swallow only the juices and soft parts, letting the chitinous shell pass out of the corners of the mouth.

During the winter 1907–8 my captive bats were kept in small glass and wire cages that were placed in a small photographic, dark room. The door was never closed tightly, except temporarily, so the darkness was not complete and ventilation was fairly good. The temperature varied somewhat but never fell below 40° F. nor rose above 65°. The animals spent most of

the time clinging to the sides of the cages near the top, but went down now and then to get water. As long as they were undisturbed they moved about little and remained in good health. Some *M. lucifugus* obtained in Mammoth Cave, November 8 were kept alive until March 26. When taken out and held in the hand or placed in a warm room and touched occasionally, their temperature gradually rose, and in from ten to fifteen minutes they usually began to creep about, and then to fly. For some reason that I have not discovered, the animals never lived long when they were disturbed frequently. From February 10 to March 3 was the longest that I was able to keep a bat in good health when using it daily for experiment. It is possible that the dry atmosphere of the steam-heated rooms is not suitable for them.

A characteristic of bats, liberated in a large room where they can fly about, is the tendency of an individual to alight frequently in the same place.

Another noteworthy tendency is that of exploring every nook and corner of a room. It results in finding any crevices through which it is possible to escape. This tendency must have been of incalculable importance to animals accustomed to spending much of their time in dark retreats, reached only through small and winding passages.

<div align="center">(To be continued.)</div>

BIOLOGICAL BULLETIN

SOME HABITS AND SENSORY ADAPTATIONS OF CAVE–INHABITING BATS. II.

WALTER LOUIS HAHN.

EXPERIMENTAL STUDIES.

I. *Avoidance of Objects.*

As early as 1794 Spallanzani experimented with bats in which one or more of the senses had been destroyed. I have not had access to the original account of his experiments. According to the account of these experiments given by Godman ('26) and Flower and Lydekker ('91), bats deprived of sight, hearing and

smell, were able to avoid objects in their way and even silken threads stretched so that there was just room for the animals to pass between, and they contracted the wings when the space was too narrow for the expanded wings to pass through. Observations on a large number of captive bats have convinced me that Spallanzani's experiments were, in some way, lacking in scientific accuracy. Not a single individual out of more than sixty belonging to five species that I have experimented with, have shown any approach to this degree of skill in avoiding objects, even with the senses all intact.

The experiments here described were made at the " University Farm " in the spring and summer of 1907, and were checked by additional ones in the laboratory of Indiana University in December of the same year. They were similar in part to those made by Rollinat and Trouessart ('00), with, however, a simpler arrangement of obstacles and with each experiment worked out quantitatively.

The experiments show that bats are able to avoid objects when flying, but that avoidance is not complete. Several senses may be of use in perceiving obstacles, and air currents perhaps guide the animals to some extent. However, destruction of the sense of sight does not seriously impair their ability to perceive objects nor does the loss of the external ears and tragi. The most important senses are located in the internal ear and any disturbance of these organs seriously impairs the animal's ability to perceive and avoid obstacles.

The following method was used: The bats were liberated in an unceiled room approximately fifteen feet wide, eighteen feet long, nine feet from floor to eaves and twelve feet from floor to the apex of the roof. Pieces of black, annealed iron wire about one millimeter in diameter were suspended from the rafters and kept moderately tight by fastening the lower ends to a cross wire five feet from the floor. On an average, there was one wire to each eleven inches of space, but they were spaced unequally, the purpose being to determine whether the bats would try to pass through the more narrow spaces or learn to select the wider ones. During a part of the experiments there was an additional row of seven short wires, alternating with the others and placed twenty inches from

the first row, but they were high in the comb of the roof, the bats seldom passed between them, and as they had no apparent effect upon the experiments they will be counted as though all were in one series.

Wires were used in these experiments in preference to larger objects because a bat will invariably try to perch on any object it strikes and it is sometimes difficult to tell whether the animal intended to perch or whether it did not perceive the object. Wires have an advantage over strings because the slightest touch causes a perceptible sound and it is not always easy to *see* whether an object is touched. Some preliminary experiments were made in April but the method of quantitative study was not decided upon until May 16, when one bat was used. Several more were tried during May and June but at this time few bats were in the cave. The experiments were therefore discontinued until later and most of them were made between August 25 and September 5.

Some of the animals were very fat and inactive during late summer and it was difficult to keep them flying. There are great individual differences and some of the experiments required six times as long as others and some bats had to be discarded for the purpose of these experiments because they would not fly at all or would make short flights in one corner of the room and not attempt to pass between the wires. The tabulated results were obtained from the use of 48 bats belonging to three species. About fifteen additional individuals and two additional species were liberated in the experiment room but are omitted from the tables because the data are incomplete. The total number of observations on avoidance is about 6,000.

The individual differences and the varying degrees of lethargy in the same individual at different times make it essential to determine the normal reactions of each animal before trying experiments under changed conditions. For this reason it was deemed necessary to test each individual in a normal and uninjured condition immediately before the experiment in which one of the senses was impaired.

The bats were captured in the cave and were generally used for the experiment on the same day, although some of them were

not used until the next day. The normal, uninjured animals were liberated in the room and their movements carefully watched. Each time one of them passed between the wires or approached quite near to a wire and appeared to dodge it was called a trial. It was at first intended to allow 100 trials for each bat but it was found that the animals were apt to become tired and refuse to fly before the experiment was concluded and the number of trials was reduced to 50 for each condition. The wings brushing against the wires, even very lightly, produce an audible sound so that it was easy to tell when the animal struck the wires.

Most of the normal bats flew about the room rapidly for a time and then began to stop frequently, alighting on the walls, the underside of the roof or objects in the room. After a period of varying length some of them attempted to settle down and it was difficult to keep them on the wing. On being driven from their perch they would make short flights only, and stop again. For reasons previously stated (p. 167) striking objects other than the wires were disregarded.

Four kinds of mutilation were employed : (1) The eyes were covered with an opaque mixture of lamp black and glue. (2) The external ears and tragi were excised close to the head. (3) The external auditory meatus was stopped with a small quantity of plaster of Paris which was allowed to harden before the bat was liberated. (4) The hairs of the body and membranes were pasted down with thick vaseline.

When the eyes were covered with the mixture of lamp black and glue, the most noticeable effect was to decrease the activity of the animal. Usually a bat so treated alights somewhere and tries to remove the substance from its eyes, using the hind foot, as the thumb and wrist cannot be brought into contact with the head. If the glue is allowed to harden somewhat before the animal is liberated, it is not so easily removed ; even then it is necessary to dislodge the bat as soon as it alights or it will finally succeed in removing the hardened glue. In every instance the animals were examined at the conclusion of the experiment to see that the covering was intact.

The 47 bats used in these experiments struck the wires 25 per cent. of the 2,350 trials recorded for the uninjured condition.

Twelve of the forty-seven were blinded in the manner previously described and given fifty trials each. In these 600 trials the percentage of hits was 21.7. However, the percentage of hits for the same twelve in the normal condition was only 23.6 per cent. as compared with 25 per cent. for the total forty-seven.

TABLE I.

AVOIDANCE OF WIRES.

Myotis lucifugus.

No. of Bat.	Condition Normal.		Eyes Covered.		Ears and Tragi Excised.		Meatus Stopped.		Hair Covered.	
	1st 25 Trials.	2d 25 Trials.	1st 25 Trials.	2d 25 Trials.	1st 25 Trials.	2d 25 Trials.	1st 25 Trials.	2d 25 Trials.	1st 25 Trials.	2d 25 Trials.
1	3	8	3	3					7 [1]	2
2	9	5	6	6			16	21	5 [1]	15
3	8	4	1	4			19	13	9 [2]	8
4	15	6					17	17		
5	8	7					17	18		
6	8	7					18	14		
7	9	6					16	15		
8	1	3								
9	8	6			9	5				
10	6	6			15	12				
11	7	5			5					
12	6	3			5	7				
13	8	6			9 [3]	5			7	4
14	8	6							15	20
15	7	4								
16	5	3								
Average No.	$7\frac{1}{16}$	$5\frac{5}{16}$	$3\frac{1}{3}$	$4\frac{1}{3}$	$8\frac{3}{5}$	$7\frac{1}{4}$	$17\frac{1}{6}$	$16\frac{2}{6}$	$8\frac{3}{5}$	$9\frac{1}{5}$
Total per cent.		24		15.3		31.4		66.6		36.4

It is therefore apparent that bats deprived of the sense of sight not only are able to avoid objects but, in these experiments, they avoided them better while blinded than they did with sight unimpaired. This does not necessarily mean that they perceived objects more readily with the eyes covered. It was noted that there was a greater tendency to avoid the vicinity of the wires when blinded. The flight seemed slower, although it could not be measured, and more care was probably used to avoid objects.

[1] Eyes freed.   [2] Meatus freed.   [3] Hair covered first.

The second condition of these experiments, the removal of the ears is also without marked effect on the perception of objects.

Five *M. lucifugus* struck the wires 31.7 per cent. of the chances as against 24.4 for the same individuals when normal, and 25 per cent. for all individuals used. Six *M. subulatus* struck 24.6 per cent. of their chances with the ears and tragi removed as against 32.6 per cent. for the same animals when normal. Four *P. subflavus* struck 20.8 per cent. when operated upon and 26 per cent. when normal.

The high percentage of strikes for *M. lucifugus* after the operation is due to a single individual which was injured in the operation. When it is omitted, the percentage for the other four is 24.3, or about that for the normal individuals. The average per cent. for all three species is 23.2 or 1.8 per cent. less than the total average. This difference is so small that it may be accidental and without significance. However, this set of experiments shows that the external ears and tragi are not necessary for the perception of objects. These results are in accordance with the conclusions reached by Rollinat and Trouessart ('00) and Merzbacher ('03).

To stop the external auditory meatus dry plaster of Paris was pressed in lightly with a pair of forceps, and then wet with a drop or two of water. The superfluous water and plaster was wiped out of the ear conch and the bat was held firmly for a few minutes until the mixture hardened. Even then the animals would break the hardened plaster from the ear if they were allowed to rest very long. They were examined at intervals and no trials were recorded in which there was a possibility of the plaster having been removed.

The results were very different from those obtained from the previous experiments. Six *M. lucifugus* struck the wires 67 per cent. of the chances. The same six in the normal condition struck but 26.3 per cent. Five *M. subulatus* struck 65.2 per cent. of chances with ears stopped and the same five normal struck 26 per cent. Five *Pipistrellus subflavus* struck 65.6 times and only 23.2 when normal. The concordance of the figures for these experiments, divided into three groups, is significant and shows that the results are not due to accident but have some common basis.

There are, however, complicating factors which make the interpretation of the results somewhat difficult since the exact way in which the ears are affected is not known. A male *M. lucifugus* used on July 15 seemed to be able to equilibrate perfectly but it flew with a heavy, uncertain flight and was never observed to dodge an object. When it came in contact with any object to which it could secure hold with its claws it clung to it, but always alighted in the position in which it happened to strike instead of reversing in the air and alighting head down. Another bat was able to right itself when tossed end over end into the air but it was never seen to dodge and it struck the wires on 66 per cent. of the trials. Others acted in a similar manner.

TABLE II.

AVOIDANCE OF WIRES.

Myotis subulatus.

No. of Bat.	Condition Normal.		Eyes Covered.		Ears and Tragi Excised.		Meatus Stopped.		Hair Covered.	
	1st 25 Trials.	2d 25 Trials.	1st 25 Trials.	2d 25 Trials.	1st 25 Trials.	2d 25 Trials.	1st 25 Trials.	2d 25 Trials.	1st 25 Trials.	2d 25 Trials.
1	5	7					18	20		
2	6	6					16	17		
3	5	11					17	15		
4	9	7					19	16		
5	5	4			1	7	17	8[2]		
6	7	5			9	9[1]			5	9
7	7	5			6	4			14	14[2]
8	6	4			7	5			9	7[2]
9	8	4			8	6			11	12[2]
10	7	8	6	6					7	11
11	9	7	10	6						
12	6	7	8	10						
13	6	5	9	8	5	9				
14	6	6								
Average No.	$6\frac{6}{14}$	$6\frac{2}{14}$	$8\frac{1}{4}$	$7\frac{2}{4}$	6	$6\frac{1}{6}$	$17\frac{2}{5}$	$15\frac{1}{5}$	$9\frac{1}{5}$	$10\frac{3}{5}$
Average per cent.		25.1		31.5		24.6		65.2		39.6

It is difficult to calculate exactly the number of probable strikes if there were no avoidance because the wires were unequally spaced and because the distance between the tip of the wings is

[1] Hair covered.

[2] Ears and tragi removed first.

less on the up and down stroke than when horizontal. The average expanse of the two species of *Myotis* is ten inches. If we deduct one inch for the contracted wings and assume the wires to be equally spaced, the probable percentage of hits is 82. There is therefore some avoidance even when the ears are stopped.

The fact that bats with the meatus plugged were able to equilibrate and alight on objects which they struck would seem to indicate that the disturbance was not a mechanical one, *i. e.*, due to the weight of the plaster or to sensations caused by its pressure on the tympanum or labyrinth, but that it was due wholly to an interference with sensation, and probably to the failure of vibrations to reach the sensory cells of the internal ear.

Table III.

Avoidance of Wires.

Pipistrellus subflavus.

No. of Bat.	Condition Normal.		Eyes Covered.		Ears and Tragi Excised.		Meatus Stopped.		Hair Covered.	
	1st 25 Trials.	2d 25 Trials.	1st 25 Trials.	2d 25 Trials.	1st 25 Trials.	2d 25 Trials.	1st 25 Trials.	2d 25 Trials.	1st 25 Trials.	2d 25 Trials.
1	5	7					23	19		
2	9	9					17	17		
3	3	6					15	18		
4	6	7					16	15		
5	2	4	2	2			16[2]	17	7[1]	4
6	5	2	5	7					8[2]	9
7	6	4	4	3						
8	7	4	7	4						
9	8	5	6	5					9[2]	5
10	11	13							10	15
11		6							8	7
12	7	11			4	8				
13	8	4			5	7				
14	9	7			6					
15	6	2			4	2				
16	5	6			12	11				
17	3	2								
18	7	12								
5										
Average No.	$6\frac{2}{9}$	$6\frac{3}{18}$	$4\frac{4}{5}$	$5\frac{1}{5}$	$6\frac{1}{5}$	7	$15\frac{2}{5}$	$17\frac{2}{5}$	$8\frac{2}{5}$	8
Average per cent.		24.4		20		26.4		65.6		32.8

[1] Eyes and ears freed.

[2] Eyes freed.

Hearing undoubtedly aids the bat to secure the flying insects on which it feeds and thus has been developed to a high degree by natural selection. The perception of a stationary object is probably due to the condensation of the air between the flying bat and the solid body that it is approaching. If hearing is relatively as well developed in a bat as smell is in a dog it is not difficult to imagine that condensation of the air so slight as to be imperceptible to the human ear will arouse sensations on the auditory end organs of the bat. It is reasonably certain that the highly modified external auditory apparatus of a bat has some important function, the exact nature of which is unknown. Flower and Lydekker ('91) state that the function of the tragus is probably to " cause undulations in the waves of sound and so intensify and prolong them." As far as I am aware, no attempt has ever been made to more definitely define the function of that organ. It seems to me highly probable that it also has a selective action, perhaps destroying waves of certain kinds and intensifying others.

It is necessary to bear in mind in discussing the senses of the lower animals that it is impossible to form any adequate conception of the sensations and mental life of the lower animals on the basis of our own. If a piano recital is incomprehensible to a Hottentot, or a snake dance to a cultured Caucasian, how much less can either hope to understand the perceptions aroused in the brain of a hound that scents a fox, or the mental processes of a bat as he circles among the tree tops in pursuit of insects ?

The body of a bat is covered with fine hairs of a peculiar structure. The membranes also support hairs, the number varying considerably in the different species. These hairs are supposed to have a sensory function. No means was devised for completely destroying the sense organs located in them without seriously injuring the animals. But they were coated with thick vaseline which pasted the hairs together and made them less sensitive to slight stimulation.

The experiments under these conditions yielded the following results : Five examples of *M. lucifugus* with the hair so coated struck 36.4 per cent. of chances. The same five normal struck 28.8 per cent. Five *M. subulatus* struck 39.6 per cent. of trials

with the hair covered, and 24.4 per cent. when normal.   For five
P. subflavus the proportions were 32.4 per cent. and 25.2 per cent.

The difference of proportion for these three species is consider-
able and there is no reason apparent.   It is not safe, however, to
infer that there is any important difference in the sensibility of
the hairs of these species for there is a large individual variation,
both the lowest and highest individual percentages being found
in *Myotis lucifugus*.

The figures indicate that the organs of touch, located in the
skin and probably associated with the hairs, are of value in en-
abling the animals to avoid objects, though of lesser value than
the auditory organs.   However, it is necessary to take into con-
sideration the mechanical effect of the vaseline in making the
wing membranes sticky.   Invariably the flight of the bat became
more labored, it stopped more frequently and was less readily
dislodged from its perch after being covered with the vaseline,
although the animals were able to equilibrate and alight on either
vertical or horizontal surfaces as well as when in the normal
condition.

In order to check the experiments made at the "University
Farm" and to determine some points that were overlooked, addi-
tional experiments were made in the laboratory at Bloomington,
in December, 1907.   In place of the wires spaced at irregular
intervals, white cotton tapes, 15 millimeters in width, were
stretched from floor to ceiling and spaced regularly, the distance
between them being 12 inches.   The average expanse of *Myotis
lucifugus* is 10 inches and there was thus an allowance for error
of 2 inches, supposing the bats aimed at the middle of the space.
However, the percentage of hits for five individuals, of *M. luci-
fugus* in 50 trials each was 58.4 when normal and 60 with the
eyes covered, as against an average of 25 per cent. in the earlier
experiments.

This discrepancy can perhaps be accounted for in part by the
method of counting hits.   When the wires were used the hits
were counted only when audible.   With the tapes it was necessary
to adopt some other method of counting and a "hit" was recorded
every time that the moderately loose tapes were set in motion by

the animal. This could happen without actual contact with the tapes. However, it is improbable that this difference in method alone would account for so great a difference in results. The greater rigidity of the wires would doubtless make them easier to distinguish if the air condensing theory be correct, but not if sight were relied on. The bats would also have less cause to avoid the tapes because striking them would cause no pain. In this set of experiments a distinction was made between "hits" in which the animal struck the tape squarely with the body or upper part of the arm, and "touches" in which the obstruction was merely brushed with the tip of the wing. The preponderance of the latter bears out the assumption that no attempt was made to avoid the objects.

In these experiments each set of fifty trials was divided into five groups of ten each, the object being to see whether there was a progressive decrease of the percentage of hits due to experience. An examination of the table shows that there is no progressive decrease either in the "hits" or "touches," nor for the normal or blinded condition.

TABLE IV.

AVOIDANCE OF TAPES.

Number of Bat.		Condition Normal.					Eyes Covered.				
		1st 10 Trials.	2d 10 Trials.	3d 10 Trials.	4th 10 Trials.	5th 10 Trials.	1st 10 Trials	2d 10 Trials	3d 10 Trials.	4th 10 Trials.	5th 10 Trials.
1	Touches.	6	5	9	3	6	6	4	5	5	6
	Hits.	1	2	1	2	6	2	4	0	3	2
2	Touches.	5	7	5	4	2	5	3	2	2	2
	Hits.	3	0	0	2	0	0	1	1	2	2
3	Touches.	6	7	3	3	9	4	3	2	7	4
	Hits.	0	1	2	2	0	2	1	2	0	2
4	Touches.	6	7	5	7	4	7	9	10	8	9
	Hits.	1	1	1	0	0	0	0	0	1	0
5	Touches.	3	2	2	3	2	6	3	1	5	4
	Hits.	1	2	1	1	1	1	2	0	0	0
Average No. of Touches.		$5\frac{1}{5}$	$5\frac{3}{5}$	$4\frac{1}{5}$	4	$4\frac{3}{5}$	$5\frac{3}{5}$	$4\frac{2}{5}$		$5\frac{2}{5}$	5
Average No. of Hits.		$1\frac{1}{5}$	$1\frac{1}{5}$	1	$1\frac{2}{5}$	$1\frac{2}{5}$	1	$1\frac{3}{5}$	$4\frac{3}{5}$	$1\frac{1}{5}$	$1\frac{1}{5}$
Average of both.		$6\frac{2}{5}$	$6\frac{4}{5}$	$5\frac{1}{5}$	$5\frac{3}{5}$	6	$6\frac{3}{5}$	6		$6\frac{3}{5}$	$6\frac{1}{5}$

Per cent. of totals for normal condition, 60.8.
Per cent. of totals for blinded condition, 60.

To determine whether there was any avoidance or whether the animals hit or missed by accident, a ball of cotton with one diameter equal to the expanse of the bat and the other slightly smaller, to compensate for the upward stroke of the bat's wing when the distance from tip to tip is somewhat less, was thrown at random at the tapes. The ball struck 82 per cent. of the trials, or approximately the calculated number, as against the maximum of 60 per cent. for the bats.

The difference is more apparent when we separate the " hits " from the " touches." For the ball the " hits " were 48 per cent. of the total chances and " touches " were 34 per cent. For the animals the percentage of " touches " in the normal condition is 48.4 and 49 with sight eliminated. On the other hand, the " hits " were 9.6 per cent. of the chances under normal conditions and 16.6 per cent. with the eyes covered. From these figures it is apparent that the animals avoid striking objects in such a way as to impede their flight much more often than they avoid brushing against them with the tips of the wings.

In the caves I have often seen horizontal scratches on mud banks or on slime-covered walls that must have been made by flying bats that were unable to completely avoid the obstacles in their path. I have not seen any evidence that they ever strike the walls hard enough to do themselves injury. The great agility with which a bat can check its flight or change its course enables it to either turn aside or take hold of an object which it strikes even if it is not perceived until the animal is almost against it. It is highly probable that the fatty pads which lie about the nostrils have a protective value and prevent injury to the animal when it strikes, head on.

The experiments described above show that bats do not always avoid obstacles in their path. Spallanzani's statement as to the accuracy with which they perceive objects in their pathway, on which a number of writers on natural history have based erroneous statements, are incorrect, at least in so far as they apply to the species studied in the preparation of this paper. On the other hand, these experiments show that bats do perceive objects that they are approaching by senses other than sight or hearing as usually understood. The most important sense organs for the

perception of objects are in the internal ear.   The hairs of the body and membranes also have a sensory function.   The external ears, the tragi and the eyes are not necessary for the guidance of the animals, although there is reason to believe that when they are flying in the light they depend, to some extent, upon the sense of sight to perceive objects.

Additional Observations.

A large brown bat, *Eptesicus fuscus*, brought into the experiment room May 2 seemed wholly unable to avoid the wires.   It flew rapidly, was not seen to dodge any obstacle, and struck the wires 67 times out of 100 chances when uninjured.   It appeared to be frightened by its unusual surroundings.

A long eared bat, *Corynorhinus macrotis*, captured May 1, struck 52 times out of 102 chances.   After it had been flying in the room for ten or fifteen minutes it began flying against the windows.   It returned to the same point time and again, striking the pane when the window was closed or the wire screen, if the window was open.   Usually it struck with considerable force and fell to the sill, but immediately got up and repeated the performance.   An adult *Myotis lucifugus* liberated in the house on April 30 acted in the same way and other individuals of both the common species of *Myotis* flew against the glass and window screen.

There were great and unaccountable individual differences in this regard.   A male *M. subulatus* on September 3 struck the screen repeatedly, both when the eyes were normal and when they were blindfolded.   Another male of the same species used on the following day flew directly toward the screen a number of times but always turned in time to avoid it.   Apparently in these instances the animals were depending upon the sense of sight in guiding their movements.   The window glass would be invisible to an animal that had never had experience with transparent objects and the wire screen was not very apparent against the background of trees among which the house is situated. The actions of the bats in flying about the room at certain times seemed to indicate that they were depending on sight for guidance in avoiding the wires.   The flight when the eyes were cov-

ered was usually slower and more cautious than when the senses were unimpaired.

In the cases where they flew against the screen that obstructed the open window, the bats may have been attracted by incoming currents of air. In experimenting with them in a closed room they almost invariably found the cracks under doors, in the sides of the room, or under the roof and the experiments were seriously delayed by a large number of the animals escaping through crevices which were overlooked or were supposed to be too small for the passage of their bodies. They always explore every corner of any compartment into which they are placed and their manner often indicates that they are attracted to an opening from a distance of several feet when the air currents are the apparent stimulus.

II. *The Formation of Associations and the Sense of Direction.*

The experiments described in this section deal chiefly with a single kind of association, namely, that of place. In studying this sort of association, data were obtained which seem to indicate the presence of a sense of direction not based directly on any of the five senses commonly recognized.

The peculiar habits of a bat make it impossible to employ the methods generally used by animal psychologists in studying the formation of associations. Bats will not go to a dish for food at regular intervals. Although they readily learn to escape from any possible opening, they do not have any adaptation for grasping which would enable them to learn to pull a string or raise a latch and so open a door.

I did not find any evidence that associations of form or color are ever formed. Such associations are hardly to be expected in animals with visual organs so poorly developed.

Sound associations are formed readily. A sucking noise made by the lips at first alarmed the animals, but they soon learned to associate it with feeding. On hearing it they would look about and snap at any object that could be mistaken for food. One individual (bat No. 2 mentioned below) was especially quick to form this association and learned to come on hearing the sound, although it did not learn to localize it definitely. Alcock ('99)

states that a hairy-armed bat, *Vesperugo leisleri* (*Pterygistes leisleri*), learned to come for food on hearing a pair of scissors clicked together.

For studying place associations the following method was used : The bats were kept in cages in the dark room as previously described. For the experiments they were taken into a well lighted room and placed in a small experimental cage made of wire cloth, the sides being of one fourth inch mesh and the top, bottom and ends of one eighth inch mesh. The dimensions were 12 by 13 by 27 inches. On one side was cut a hole seven inches square. This opening was closed with a door made of the same material as the side, and overlapping the edges an inch all around. It was fastened with a wooden latch on the outside. A piece of white cloth, three inches square, was fastened inside the cage, near the upper left corner of the door.

The bat to be used in the experiment was placed on the floor of the cage near the middle. All of its movements were carefully recorded during the whole time it was in the cage. As soon as it touched the cloth while following its natural tendency to explore every part of the cage, the door was opened and a meal worm was offered it with a pair of forceps.

Animals that had never been handled were usually frightened away by thrusting the hand toward them and moreover they did not know how to eat the meal worms. Therefore it was necessary to use bats that had been in captivity for some time and had learned to eat the food offered them.

As soon as the animal under observation had eaten the food given it, it was again placed on the bottom of the cage and given another chance to come to the same place for a worm. The time required was carefully noted and also the movements of the animal which did not result in bringing it nearer to the food.

The curves given by Porter ('04) for similar observations on English sparrows, and Kinnaman ('02) for monkeys, are fairly uniform after the animal had found the food once or twice. The animals used by these observers apparently responded in about the same way to the same stimulus in all instances where there was no disturbing factor. The reactions of a bat are much less constant. When placed in the experimental cage it sometimes

goes at once to the spot where food is given. At other times when it should be about as hungry, it sits quietly on the floor for five minutes or longer and then goes without error or hesitation for the food. Even when it wanders about the cage instead of going directly to the feeding place, it cannot be asserted that the animal has forgotten where it must go for food; the impulse to explore the cage may be stronger than the hunger impulse.

The erratic behavior of bats makes it impossible to tabulate the results or to plot a curve of the time of response that will give a correct idea of the behavior of the animal. For this reason the record of the observations for one bat will first be given in considerable detail, and the conclusions will be stated afterward.

This bat, a female *Myotis subulatus*, recorded as No. 2 in my experiments, was obtained in Shawnee Cave at Mitchell on December 8, 1907. It was kept in a small cage with other bats in the dark room and was occasionally taken out and fed meal worms and allowed to fly about the laboratory. It could always be easily aroused from its dormant state and was unusually alert and active.

In the following records it is to be understood, unless otherwise stated, that the time recorded is that from the instant the animal was released in the middle of the cage until it touched the cloth.

This bat was first placed in the experimental cage on February 7, at 2 : 06 p. m. (1) It ran and flew about in all parts of the cage and in three minutes reached the cloth and took it in its teeth, probably mistaking it for food because it moved when touched. (2) Was fed and remained quiet for a time, then left and came back and was fed at 2 : 27. (3) Put on bottom of cage and came back in 1½ minutes but left before it could be fed. (4) Back and fed 3 minutes later. Crawled away and became quiet and was taken out.

Was not put in again till February 10, at 3 : 39. First time came to cloth in 6 minutes; second time in 1½ ; third in 1 ; fourth in 2 ; fifth in 70 seconds ; then in 40 seconds. Experiment terminated.

It is evident that the association had been definitely formed at this time or after a total of ten trials, the first four of which occurred three days earlier than the last six.

February 11 : (1) Put on floor of cage at 3 : 25. Flew up to cloth in 20 seconds. (2) Flew up to front, went across to cloth and began pulling at it in 17 seconds. (3) Flew directly to cloth after ten seconds. (4) Looked about, flew to right end of front, then ran to cloth in 30 seconds. (5) Hesitated and looked about, then flew to front and reached cloth in 30 seconds. (6) Was quiet, then turned and flew directly to cloth in 40 seconds. (7) Went to corner of cage, hesitated, then flew to front and went directly to cloth in 35 seconds. (8) Flew directly to cloth in 10 seconds. (9) Did not move for 75 seconds, then turned partly around and flew directly to cloth. (10) Looked around, scratched itself and washed its face, then after 2½ minutes, flew without hesitation to cloth.

Was not taken out of the living cage on February 12.

February 13 : (1) Put in cage at 3 : 58½. Flew to end of cage and climbed across to cloth in one minute. (2) Flew to right front, walked across and was fed in 20 seconds. (3) Looked around and flew directly to cloth in 12 seconds. (4) Turned around several times, flew into corner and went to cloth in 45 seconds. (5) Was quiet an instant, turned and flew to cloth in 45 seconds. (6) Put on floor, flew to front of cage near cloth, turned toward it but stopped, looked about, then cleaned its fur and became quiet ; nearly five minutes after being put on the floor it again began to look about, then went directly to cloth and was fed. (7) At once ran to front of cage and climbed it but did not go to cloth till 3 minutes later. (8) Remained quiet a minute, then climbed up in corner nearest cloth and rested a minute, then went directly to cloth. (9) Remained quiet on floor for a minute, then flew to end of cage and remained for some time, when the experiment was discontinued.

February 14 : There were no peculiarities in its activity. The times for the trials were as follows : (1) 15 seconds ; (2) 20 seconds ; (3) 10 seconds ; (4) 7 seconds ; (5) 20 seconds ; (6) 30 seconds ; (7) 12 seconds ; (8) 45 seconds ; (9) 45 seconds ; (10) failure, the animal settled at one end of the cage and remained there until taken out.

Was not put in the experimental cage nor fed on the fifteenth, sixteenth, or seventeenth.

February 18 : (1) Put in at 2 : 47 and flew about the cage, bumping the sides; rested on the bottom, then flew to front and went to cloth in 4½ minutes.   (2) Put on floor, rested on end of cage, then went to cloth in 6¼ minutes.   (3) Flew to front and went across to cloth in 20 seconds.   (4) Flew to door of cage in 10 seconds, but seemed to have learned that food came in through door and waited there.   Got to cloth in one minute.   (5) Sat on floor without moving for 2 minutes, then flew directly to cloth but started across to edge of door before it could be fed.   (6) Was quiet 1 minute, then flew directly to front of cage and reached cloth in 70 seconds but again turned to door.   Was put back on floor without being fed, started away but came back and began chewing cloth and was fed 2½ minutes after being first put on the floor.   (7) Remained quiet 3 minutes, then flew to front and started toward cloth but stopped and cleaned its fur, remaining there 15 minutes ; then turned suddenly and went directly to cloth.   (8) Remained quiet 1 minute, then flew directly to cloth.   (9) Remained on floor for 10 minutes and then was taken out.

February 19 : (1) Put in at 2 : 05, seemed rather torpid ; walked across cage, then remained quiet until 2 : 13 when it flew directly to cloth.   (2) Flew to front of cage and started to cloth in 45 seconds but stopped, 20 seconds later went to it but heard my hand at door and started to it ; was not fed ; 1 minute later, turned and went again to cloth and was fed.   (3) Remained quiet, then flew to front and went directly to cloth and pulled at it with its teeth in 2½ minutes.   (4) Was quiet, then flew directly to front and went to cloth in 1 minute.   Was beginning to turn toward door again when fed.   (5) Cleaned its fur and was quiet, then flew directly to cloth in 4½ minutes.   (6) Was quiet, then flew directly to cloth after 7 minutes.   (7) Quiet, flew directly to cloth after 3 minutes.   (8) Quiet, flew directly to cloth after 2 minutes.   (9) Quiet, flew to front and went directly to cloth in 1¾ minutes.   (10) Quiet, flew to front near cloth in 2 minutes, but remained there cleaning fur 6 minutes longer when it turned and began to pull cloth with its teeth.   (11) Flew directly to cloth after 1 minute.   Taken out.

For February 20 the times are : (1) 1¼ minutes ; (2) 15 sec-

onds; (3) 2½ minutes. (4) Quiet 12 minutes, was disturbed and then went to the cloth in 2 minutes. (5) Quiet 5 minutes, disturbed, then responded in 1 minute. (6) Quiet 11 minutes; disturbed, then went to cloth in 3 minutes. (7) 45 seconds. (8) 8 seconds. (9) 75 seconds. (10) 45 seconds.

February 21 : (1) 75 seconds; (2) 45 seconds; (3) 1½ minutes. (4) Became quiet for 8½ minutes; disturbed, then went to cloth in 1 minute ; (5) seven seconds ; (6) 12 seconds. (7) Quiet for 5 minutes. Disturbed, then went slowly to cloth in 1 minute. (8) Quiet; disturbed, then became quiet again and was disturbed a second time. Went by indirect route to the cloth 2½ minutes after second disturbance. (9) Ran to front of cage and climbed to cloth in 20 seconds. Dropped the worm given it and then turned around and took hold of the cloth with its teeth. (10) Became quiet; was disturbed after 7 minutes and flew directly to cloth 25 seconds later.

February 22 : (1) Put in at 1: 57. Flew directly to cloth and pulled at it with teeth in 10 seconds. (2) Flew directly to cloth in 15 seconds. These two trials show that, as on several preceding days, there was no error in finding the cloth. There has been delay due to inhibition of the stimulus or the lethargy of the animal but it has been finding the piece of cloth quickly whenever it was trying to find it.

At this point the bat was taken out of the cage and placed temporarily in a box. The cage was rotated through 180 degrees so that the front now faced the west instead of the east. The observer's chair was also moved to the west side and a box in which there was another bat moving about was moved from the east side where it had been kept during the greater part of the experiments, to the west side. It is to be remembered that the door of the cage is in the middle upper part of the front and the cloth is at the upper, left or back edge of the door, 7 inches from the left end of the cage and 20 inches from the right end.

After the cage was reversed and the observer again seated in front, the bat was placed in it.

Trial (1). — Was placed on the floor facing the cloth ; looked about, slowly turning its head, then turned the body and *flew directly to back of cage at a point about 7 inches from the right end*

*or the same absolute spot that it had been accustomed to go to, but
a place diagonally across the cage from the piece of cloth.* Re-
mained there for 7 minutes. (2) Put on floor facing cloth again
and looked about, then turned and flew to same point in back
in 50 seconds. Seemed to be looking about for cloth, then
became quiet. (3) Again put on floor facing cloth, turned and
flew to middle of back in 75 seconds and climbed all around over
that part of the back of cage. (4) Remained quiet 4 minutes, then
turned and flew to same spot as last time ; looked and crawled
about, then became quiet. (5) Flew to back in 70 seconds and
settled down without crawling about. (6) Flew to back in 75
seconds, looked about very little, then became quiet. (7) Put
on floor very near cloth, was quiet, then flew directly to back in
60 seconds ; climbed and looked around all over back before
settling down. (8) Looked around, then turned and flew di-
rectly to back, climbed about on back and then became quiet.
(9) Remained quietly on floor, then flew to back in 2½ minutes
and climbed about over it. Flew to lower right front (possibly
attracted by squeakings of another bat in a box near there).
Was quiet, then went to back of cage again and climbed about
over that ; it finally flew to right front corner and from there to
the floor where it rested. (10) Flew to back at right of middle
and became quiet.

At this point in the experiment the bat was taken out and the
cage was turned to its original position. (1) The bat was again
placed in the middle of the floor and crossed back and forth sev-
eral times, then flew to front near cloth in 75 seconds and began
pulling at it violently. (2) Flew to cloth in 5 seconds. (3)
Flew to cloth in 20 seconds. (4) Flew to cloth in 12 seconds.
(5) Flew to cloth in 25 seconds. (6) Remained quiet on the
floor, then flew to cloth in 1½ seconds. (7) Flew near cloth
and went to it in 30 seconds. (8) Flew near cloth and went to
it in 50 seconds.

On the following day the bat was again placed in the cage in
its original position, *i. e.,* the front to the east, and on the ten
trials of this day it went quickly and without error to the cloth.
Before any other experiments could be made with this animal,
it escaped from its cage and could not be recaptured.

Four other bats were used in the same kind of experiments between February 7 and March 6. The details of these experiments are, in general, similar to those outlined above. Each of the bats died before the observations were completed.

Bats numbers 4 and 5 both of which were female *Myotis lucifugus*, were used with a piece of bright carmine-red cloth, four by five inches square, in the cage instead of the smaller piece of white cloth. In the case of bat No. 4 the cage was reversed on the second day, or after the animal had been fed at the cloth only 13 times. The association had been quite firmly fixed, however, and the bat went to the back of the cage eight successive times after it had been reversed before it wandered about sufficiently to find the cloth. When it did get to it, it seemed to remember the place and took the cloth in its teeth. It was fed here five times but showed some confusion in finding the place and several times went to the back. The next day it also appeared confused when first placed in the cage and sometimes went to the cloth and sometimes to the back. The following day it seemed to be sick and died two days later.

Results of the Experiments on Association and the Sense of Direction.

These experiments show that visual associations are formed slowly or not at all. Sound associations are formed more readily. Tactile associations were not isolated from others but probably enter into the perceptions which lead to finding the cloth as the animals seemed to have the cloth, as well as the location of it, associated with obtaining food.

The facts relating to the sense of direction will now be taken up. The bats were fed meal worms while they rested on a piece of cloth. The cloth became soaked with the juices of the worms and it also acquired the characteristic odor of the bats to a sufficient degree for the human nose to detect it. The bats did not rely upon the sense of smell for finding the place or they would have reached it without error.

The room in which the experiments were conducted was not as free from noise as might have been desired. However, it was a basement room with thick walls and there was generally no one

except myself in the room or adjoining halls, and outside noises were not heard to a large extent. The only noises recurring with any degree of regularity in the room were those made by the steam in the heating pipes. These could have no direct association with the giving of food while the movements of the observer near at hand did have such an association and these were perceived by several of the animals at times, as when they left the cloth and started toward the sound of the opening door. Therefore sound cannot be considered as a factor in guiding the bats to the back or front of the cage.

Taste and touch may also be counted out, because, if they entered into the food associations at all, they would each tend to guide the animal toward the cloth.

It is not possible to say with so much assurance that sight is not a factor. It was possible for the animals to look through the sides of the cage, but there were no conspicuous objects near and the door of the cage with its latch, and the white or red cloth, were much more noticeable than anything else in sight.

In describing the action of the bat in the cage I have said in a number of places that it "looked around," but it is not certain that this action was really for the purpose of seeing. In a number of trials the animals were so placed that they faced the cloth and if they had been looking for familiar objects as landmarks to guide them to the food they would have noticed it first of all and would have gone directly to it.

The only way in which it seems possible that sight could have aided in their orientation is through the direction of the rays of light. This is not probable because the room was well lighted by windows on two sides and the experimental cage always stood back out of the direct sunlight and also out of the shadows. Moreover, we should not expect to find that animals accustomed to spending all their lives in total darkness or twilight, would depend upon the visual sense for orientation.

While it must be admitted that the experiments did not exclude every possibility of some effective sensations being received through the five senses we commonly know, yet it is not possible to fully account for the behavior of the animals in the experiments above described on the basis of these senses alone, unless

they are developed to a degree which we know nothing about from direct experience.

Watson ('07) found that the ability of white rats to learn a maze was not impaired by the destruction of either the eyes, the olfactory lobes, the middle ear or the vibrissæ, or by anesthetizing the paws or nose, or eliminating temperature and air currents. When the maze was rotated through an angle of 90 degrees, they were confused, but when it was rotated through 180 degrees they were again able to find their way. Watson believes that "static sensations or some non-human modality of sensation" are necessary to explain the behavior of these rats.

Watson and Carr ('08) believe that in the white rats, orientation is attained by traversing a unit of the maze. In man, a train of acts which have become habitual may be set off by some visual or other sensory impulse. In the lower animals such acts may be set off by a "kinæsthetic sensation," such as traversing a unit of the maze and getting the appropriate "feel" of direction from some combination of motor impulses or acts.

Bats are more difficult to work with than rats because their reactions, always uncertain, are seriously disturbed by any kind of operation. Those that I have had have also lacked vitality and have died before extensive experiments could be completed. However, the experiments here described seem to warrant the assumption that they also have something akin to "static sensations" which enables them to retrace their way to a point at which they have been before, without depending on the other five senses.

It is not the purpose of the present paper to discuss the nature of this sense. It may be the same as the "kinæsthetic" sense of Watson. However it is not necessary for a bat to perform an act similar to that of the rats traversing a unit of the maze in order to obtain orientation. The only movements of the bats which seemed to have any connection with orienting was a slow turning of the head in various directions. The purpose of this I could not determine. It is conceivable that if the sense of location is situated in the semicircular canals, a rotation of the head might arouse various sensations, one of which would serve as a clue to position.

There is reason to believe that bats have good memory. On

one occasion a male, *M. lucifugus*, that I had marked by excising the right tragus, escaped through a small crack under the door into another room and thence to the outside through one of several small holes. A few days later I found it in the cave and brought it to the room again, and liberated it.

It circled twice about the room and then dropped to the floor near the door and started directly for the crack and escaped from the house before I had a chance to stop it. Several days later it was recaptured a second time and turned loose in the same room. It started at once for the crack under the door. The crack had now been stopped so that it could not get out, but it ran about in that corner and for several days, whenever liberated in the room it repeatedly went to the place where it had escaped before.

Certain bats, released in a room, show preference for alighting in a particular spot while other individuals select other spots. To illustrate, two bats were allowed to fly about a room lighted by seven windows, all of which received about equally strong light. Each bat alighted a number of times. One of them selected the casing of window number two 12 per cent. of the times and all other windows 12 per cent. Another bat selected window number five 28 per cent. of the times and did not go to window number two at all. Other instances could be cited illustrating the same point. The bats apparently find a place suitable for resting by accident the first time and later return to it because it is remembered.

In experimenting with the bats in the cage, I found that they also learned by accident to find the place where food was to be obtained. When food was once associated with a certain place the animals very quickly learned to go back there. After they once learned the association it remained very persistently. In the experiments with bat No. 2, outlined above, it was so persistent that it prevented finding a new place in ten times the number of trials required the first time.

Memory in all of these cases is doubtless below the realm of consciousness and akin to that which in man is rendered subconscious through habit. Some sort of a memory is absolutely necessary in order to make a sense of direction of any value to

the animal. It is necessary that a bat "remember" the points at which it has been or a sense of direction would not help to orient it.

The sense of direction in these bats may very probably be accounted for, at least in part, by the high development of associative memory. A man can learn to go about a house and make all the turns correctly through habit and with little or no dependence on his senses. In his case it has probably required long experience and many repetitions of the act. In the bats, an act is learned very much more quickly and it is possible that one or two repetitions may even be sufficient to render the performance automatic. If this is true, the ability of the animals to find a place at which they have once been, may be based neither on a sixth sense, nor directly upon any of the five senses, but upon associative memory and quickness in forming habit.

The utility of a sense of direction to bats is so apparent as to scarcely require discussion. It is impossible for sight to be of any service in helping them to find their way in the caves. Outside noises do not go in far and few noises originate there, so that hearing can be of little service in orienting them.

It has been suggested (Blatchley, '96) that air currents may guide them to the mouth of a cave, but this is to me inconceivable. Not only does the direction of the current change in the principal passages but there are always eddies in the chambers and tortuous passages which would tend to confuse rather than help them. The only odors are the constant ones characteristic of a cave and since the bats pass through the air and not along solid surfaces their own odor is not left with a sufficient degree of permanence to be of service in guiding them.

But if a bat have a sense of direction well enough developed to guide it in retracing its way, it would have an immense advantage over other animals of similar habits that lack such a sense. Thus natural selection would foster and improve it.

CONCLUSIONS.

Bats are separated from all other mammals by a number of morphological peculiarities which are correlated with the adaptation for flight.

They have no nests, dens or fixed homes.   The species studied stay in the caves during the greater part of their existence. They usually go in far enough to be in a constant temperature and total darkness but do not select their resting places with reference to the size of the cave, the nature of the opening or the amount of moisture.

They have few enemies.   Consequently fear is but little developed.

About five sixths of a bat's entire existence is spent in a dormant condition.   This condition is not dependent upon temperature or season but upon the condition of metabolism ; a large amount of fat is favorable to torpor.

In the caves, where conditions of light and temperature are constant, bats come to the cave entrance at irregular intervals. The length of time between these intervals depends upon the amount of surplus fat stored in the body.

They leave the cave only when favorable conditions of light and temperature prevail, and go back to the interior of the cave if the light is too intense or the air too cold.

Food consists of insects that are caught on the wing.

Several senses aid in its perception.   Smell and taste are of no use for this purpose.   Sight may aid to some extent.   Hearing and the tactile sense are chiefly relied on to perceive and locate food.

Bats are more helpless on their feet than most birds.   In the air they have greater agility.

They can check their momentum very quickly.   In flight, they can secure hold of a surface, only slightly rough, with a single thumb or with one foot.

The breeding habits of our species are not well known.   They mate in the fall and the young are born early in the summer. Breeding females leave the caves during the period of gestation and rearing the young.

The sexes do not segregate while they remain in the cave.

Bats in captivity do not readily learn to pick up food from the floor of the cage.   They will eat food presented to their mouths and will go to a dish for water.

They do not live well in captivity except when in the quiescent state.

Experimental studies show that neither sight nor the external ears and tragi are necessary for the perception of obstacles during flight.

The body hairs probably have a sensory function.

Obstacles are perceived chiefly through sense organs located in the internal ear.

Perception is probably due to the condensation of the atmosphere between the moving animal and the object it is approaching.

Bats show a remarkable ability to return to a particular spot for food or for the purpose of escaping from an enclosure.

It is difficult to explain how they find their way by means of the five senses familiar to us.

The presence of a sixth sense, that of direction, will explain all of the facts.

It has not been conclusively shown that such a sense exists. If it exists in any animals we should expect to find it in bats. Their habits are such that a sense of direction would be of advantage to them in the struggle for existence.

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ON THE RELATION OF RACE CROSSING TO THE SEX RATIO.

MAUD DeWITT PEARL AND RAYMOND PEARL.

INTRODUCTION.

There would appear to be widely prevalent among practical stock breeders an opinion that the relative proportion of the sexes may be influenced by the method of breeding practiced. As evidence of the existence of such an opinion two citations will suffice. Others might be given. Davenport in his memoir on "Inheritance in Poultry,"[1] introduces a section on "Sex in Hybrids" (p. 97) with the statement that : "There is a widely held and frequently expressed opinion that hybrids show an excessive proportion of males." He further says that : "Bateson and Saunders probably have this in mind in their statement — 'the statistical distribution of sex among first crosses shows great departure from the normal proportions.'" No support is given to the view that hybrids show an undue proportion of males by Davenport's own statistics, the general conclusion being that : "The exceptions to the law of equality of sexes in hybrid offspring are . . . individual and not of general significance."

It is a matter of interest to note that while the opinion appears to be widespread that the kind of breeding practiced influences the sex ratio there is not entire uniformity as to what the influence of a particular method of breeding on sex is. Thus one would infer from a statement in a recent work by Müller[2] that it has been generally held by continental breeders, at least, that *inbreeding* tends toward the production of an unduly large proportion of males. Müller[2] (*loc. cit.*) in discussing the experiments of Schultze (*cf. infra*) makes the following statement concerning certain of that author's results : "Das Verhältnis der beiden Geschlechter war vielmehr bei strengster Inzucht (Paarung nur

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[1] Carnegie Institution of Washington, Publication No. 52, 1906.
[2] Müller, R. "Biologie und Tierzucht." Gedanken und Tatsachen zur biologischen Weiterentwicklung der landwirtschaftlichen Tierzucht. Stuttgart (Ferd. Enke), 1905. Pp. 96.

mit Bruder, Enkel, Urenkel, Vater und Grossvater) ein sehr verschiedenes, ja in einigen Fällen kamen sogar in der dritten Geschlechtsfolge, *ganz in Gegensatze zu der alteren Annahme,*[1] überwiegend weibliche Nachkommen zur Welt."

Investigations systematically directed towards determining in what way and to what extent either hybridizing or inbreeding affect the sex ratio are very few in number.   Davenport (*loc. cit*), from a tabulation of the sex of 377 fowls reaches the conclusion already stated regarding the influence of hybridization.   Schultze[2] has studied in mice the effect of inbreeding of various degrees including the closest " Inzestzucht " on sex determination, and reaches the conclusion that in general it has no effect.

The search for factors which may determine or influence sex is being actively prosecuted by experimental biologists.   Any data tending to throw light on the significance of any supposed sex-influencing factors can but be welcome.   The quotations from the literature which have been given suffice to indicate that the character of a mating must at least be accorded the place of a "supposed " sex-influencing factor.   It is the purpose of the present paper to exhibit and discuss certain data which have a direct and definite bearing on the question of the significance of this factor in the case of one organism, namely, man.

The data which form the basis of this paper are extracted from the published vital statistics of the city of Buénos Ayres.   For nearly twenty years past this city has maintained an elaborate system of municipal statistics.   Indeed its system might in many respects well serve as a model.   It is doubtful whether the statistics of any other city or country surpass those of Buénos Ayres in completeness and accuracy.   These records are published in annual volumes, of which fifteen have appeared.   The statistics of births given in these volumes are particularly detailed.   Among other matters of general biological interest there is given each year a table setting forth the number of births occurring in the year covered by the volume, classified in such way that it appears for each child born whether it was (*a*) male or female, (*b*) legiti-

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[1] My italics. — R. P.

[2] Schultze, O.   " Zur Frage der geschlechtsbildenden Ursachen."   *Arch. mikr. Anat.*, Bd. 63, Heft. 1, 1903.

mate or illegitimate, and (*c*) what was the nationality of each of its parents. Furthermore it should be said of these statistics that they are *registration* figures and not *census* returns. That is to say, they are definite *records* of events, each event being recorded when it happens, not more or less inaccurate counts made a long time after the event. Of the substantial accuracy of these figures there can be no doubt.

As is well known, Buénos Ayres is a city having a population which is racially very heterogeneous. For a decade and more past there has been a large Italian immigration. Also there has been extensive Spanish immigration. Representatives from other nations have come in in smaller numbers. From the statistics of birth above alluded to it is possible to determine what has been the sex of the offspring of each of these racial groups in pure matings and when crossed with native Argentine stocks. For the purpose of the present study the birth statistics of the ten years 1896–1905 inclusive have been used. The following matings have been considered :

Argentine	♂	Argentine	♀
Italian	♂	Italian	♀
Spanish	♂	Spanish	♀
Italian	♂	Argentine	♀
Spanish	♂	Argentine	♀

Data are available for other matings but it has not seemed advisable to deal with any yielding less than 8,000 offspring in the ten years. The inquiry has been further limited to legitimate births, because of the uncertainty which must always exist in the great majority of illegitimate births as to whether the putative father is the actual one. With these restrictions the number of separate offspring dealt with in this study approaches a quarter of a million (exactly 219,516).

These statistics have been studied with the purpose of obtaining answers to the following questions :

1. Is there a tendency towards an excessive production of offspring of one sex (either male or female) in cross as compared with pure matings, among the human racial stocks under consideration ?

2. If such a tendency appears to exist is it (*a*) uniformly shown in all the matings considered, and (*b*) numerically great enough in amount to be considered significant when tested by probable errors ?

DATA.

The raw material on which this paper is based is set forth in Table I. The figures are extracted from Volumes VI. to XV. inclusive of the *Annuaire statistique de la ville de Buénos-Ayres.*[1]

TABLE I.

SEX DISTRIBUTION OF LEGITIMATE BIRTHS.   RAW DATA.

Nation-ality of Parents.	Argentine ♂ Argentine ♀		Italian ♂ Italian ♀		Spanish ♂ Spanish ♀		Italian ♂ Argentine ♀		Spanish ♂ Argentine ♀	
Year.	♂ ♂ Born.	♀ ♀ Born.	♂ ♂ Born.	♀ ♀ Born.	♂ ♂ Born.	♀ ♀ Born.	♂ ♂ Born.	♀ ♀ Born.	♂ ♂ Born.	♀ ♀ Born.
1896	1,597	1,654	5,326	5,455	1,814	1,695	939	932	349	411
1897	1,722	1,712	5,740	5,499	1,767	1,728	1,060	968	431	394
1898	1,922	1,773	5,765	5,703	1,805	1,695	1,152	984	431	420
1899	1,980	1,945	5,770	5,743	1,887	1,790	1,168	1,100	478	417
1900	2,038	1,950	5,070	5,620	1,809	1,784	1,126	1,064	458	411
1901	2,163	2,099	5,923	5,771	1,879	1,806	1,178	1,192	461	421
1902	2,189	2,100	5,736	5,597	1,837	1,781	1,204	1,189	463	438
1903	2,277	2,200	5,341	5,133	1,780	1,702	1,214	1,127	467	448
1904	2,352	2,368	5,419	5,240	1,952	1,723	1,345	1,215	521	460
1905	2,533	2,317	5,507	5,409	2,093	1,940	1,294	1,277	516	468
Totals	20,773	20,118	55,597	55,170	18,623	17,644	11,680	11,048	4,575	4,288

It is at once apparent that these statistics show essentially the same relation of the sexes as that usually found when large numbers of human births are examined, namely, a preponderance of males.   The extent of this preponderance may be shown best by putting the data in the form of sex-ratios.   In this paper the sex ratio will be taken as the number of males to each 100 females. The sex ratios deduced from the totals of Table I. and their probable errors are given in Table II.   It does not appear to be necessary or advisable to deal with the single years separately. The method of determining the probable errors of the sex-ratios was to determine first for each mating the probable error of the absolute frequency of males, considering this as a simple class

[1] Published by the Direction générale de la statistique municipale, Buénos Ayres.

frequency.   It has been shown[1] that if y_s be any class frequency within a sample containing m individuals altogether, then

$$P \cdot E \cdot y_s = .67449 \sqrt{y_s \left(1 - \frac{y_s}{m} \right)}.$$

From the "absolute" probable error so obtained the probable error of the sex-ratio is easily deduced.

TABLE II.

MALES TO 100 FEMALES FROM TOTALS OF TABLE I.

Mating.			Sex Ratio.	Mating.			Sex Ratio.
Argentine ♂	Argentine ♀		103.26 ± .34	Italian ♂	Argentine ♀		105.72 ± .46
Italian ♂	Italian ♀		100.77 ± .20	Spanish ♂	Argentine ♀		106.69 ± .74
Spanish ♂	Spanish ♀		105.55 ± .36				

From this table the following points are to be noted :

1. The number of males to 100 females varies between approximately 101 and 107 in the different matings.   There is an excess of males in every case.   Further, this excess is significant in amount as is indicated by the probable errors.   The present statistics agree with other large collections of data regarding the sex-ratio of human births.   There appears to be no doubt that a tendency towards the production of a greater number of males than of females is normal for Caucasian races at least.

2. The sex-ratio is in each case higher for the cross matings than for the pure.   That is, there are more males per hundred females produced when the parents are of different racial stocks than when they are of the same.

The answer to the first question propounded above (p. 196) then is that there is a definite tendency towards an excessive production of male offspring in cross as compared with pure matings in the data here considered.   Further, it appears that within the limits of the present material this tendency is uniformly exhibited in all the matings.

Attention may next be turned to the second part of the second question, which may now be put as follows :

[1] Editorial — "The Probable Errors of Frequency Constants," *Biometrika*, Vol. II., p. 274.

Is the excess of male births in cross matings numerically great enough to be considered significant in comparison with the probable errors involved?   The evidence on this point is presented in Table III., which compares the sex-ratio for each cross mating with that for each of the two pure matings related to it.   The last column of the table gives the ratio of the difference in each case to the probable error of the difference.   In interpreting this last column it will be remembered that a difference which is three or more times as large as its probable error is to be regarded as significant ; a difference which is between two and three times its probable error is probably significant ; while a difference less than twice its probable error when taken by itself is probably not significant.   In general, the technical biometrical use of the term " significant " intends to convey the idea that the odds are so great as to amount to practical certainty that a so-called " significant " result did not arise simply as a purely chance effect of random sampling, but represents a direct causal nexus between phenomena.

Table III.

COMPARISON OF THE SEX-RATIOS OF THE OFFSPRING OF PURE AND CROSS MATINGS.

Matings.		Sex Ratio.	Difference / P.E. of Difference
Italian ♂	Argentine ♀	$105.72 \pm .46$	
Italian ♂	Italian ♀	$100.77 \pm .20$	
Difference		$4.95 \pm .50$	9.9
Italian ♂	Argentine ♀	$105.72 \pm .46$	
Argentine ♂	Argentine ♀	$103.26 \pm .34$	
Difference		$2.46 \pm .57$	4.3
Spanish ♂	Argentine ♀	$106.69 \pm .74$	
Spanish ♂	Spanish ♀	$105.55 \pm .36$	
Difference		$1.14 \pm .82$	1.4
Spanish ♂	Argentine ♀	$106.69 \pm .74$	
Argentine ♂	Argentine ♀	$103.26 \pm .34$	
Difference		$3.43 \pm .81$	4.2

From this table it appears that the excess of male births in the cross matings as compared with the pure is in general large in proportion to its probable error.   In only one out of the four

possible comparison cases is the difference less than four times its probable error. In that case (Spanish-Argentine and Spanish-Spanish) the difference is 1.4 times its probable error, and could not, taken by itself, be considered significant. Taking into account, however, the facts that (*a*) the difference is of the same sense as the other differences in the table and (*b*) that it is larger than its probable error the general conclusion reached from the other figures is not vitiated. This conclusion is that within the limits of the present material *there is evidence of the significantly greater proportionate production of males in the offspring from matings involving different racial stocks than in the offspring from matings in which both parents belong to the same racial stock.*

Discussion.

The data which are set forth in the tables given above appear to lead clearly to the conclusion which has been drawn from them. This conclusion, however, is merely a statement of fact. In interpreting it it remains to consider two points. The first of these is as to whether there are limitations or fallacies in the data themselves which invalidate the conclusion to which they appear to lead. The second is as to what is the meaning of the facts implied by this conclusion supposing it to be true. One cannot be too cautious in drawing conclusions from human vital statistics of whatever kind. Vital statistics notoriously abound in pitfalls. In a critical examination of the data with a view to possible criticism and interpretation the following points suggest themselves :

1. That the material is not sufficiently extensive. It might conceivably be maintained that if a larger number of births were to be dealt with they would show a different result. For two reasons such a consideration appears to have little weight. In the first place the number of births included in the statistics is extremely large as measured by biological standards. The statistics include upwards of 200,000 births. In the second place the probable errors of the sex-ratios indicate how literally enormous are the combined odds against such a consistent system of differences as that shown in Table III., arising fortuitously. In this connection it may be said that the work was begun in the

first instance with the statistics for three years (1903, 1904 and 1905) only. The figures for these years led to exactly the results which have been shown above. The figures for the seven previous years were then taken into the calculation to see whether they would confirm or reverse these results. That they confirm them is clear.

2. That the inclusion of living births only in the statistics influences the result. That statistics of sex should theoretically include still-born as well as those born living is obvious. The still-born would have been included in the tables of this paper had it not been for the fact that the original material was tabulated in such way as to render it impossible to include them. A little consideration shows, however, that the absence of still-born does not sensibly affect the conclusion drawn from the present statistics. It is a well-known fact that among still-born children the proportion of males to females is very much greater than among living born. It does not seem necessary to cite evidence of this fact ; all large collections of birth statistics show it. Pains have been taken to make sure that the records of still-born in Buénos Ayres form no exception to the general rule.

Now there are three possibilities respecting the distribution of still-born young among the offspring of the cross and pure matings discussed in this paper. These are :

(*a*) That still-births are distributed *pro rata* among cross and pure matings. This is the most probable supposition. It would be expected on general grounds that in the long run there would be substantially the same number of still-births among a given total number of births whether this total originated from cross or pure matings.

(*b*) That a relatively larger number of still-births originate from pure than from cross matings.

(*c*) That a relatively large number of still-births originate from cross matings than from pure.

It being a fact that still-births show a high sex-ratio it is evident that a distribution of such births in accordance with (*b*) could alone tend to reverse the conclusion reached from statistics which leave these births out of account. In case they were distributed as in (*a*) or (*c*) their inclusion would simply make

more pronounced the results found in their absence. It appears highly probable on general grounds that if still-births are not proportionately distributed among cross and pure matings there is somewhat more likely to be an excess of such births arising from cross (*i. e.*, according to (*c*)) than from pure matings (*i. e.*, according to (*b*)). It is hardly conceivable that there could be a steady tendency for a sensibly greater number of still-births to occur when both parents are of the same nationality than when they are of different nationalities. If this be granted then it must also be granted that the non-inclusion of still-births in the present statistics cannot be adduced as an explanation of the observed preponderence of males in the offspring of cross matings.

3. That a different age distribution of the parents in cross as compared with pure matings may account for the observed preponderance of male births from such matings. In a population such as that here dealt with it is undoubtedly true that the males in the cross matings (being for the most part probably immigrants) are on the average somewhat older than those in the pure matings. It might conceivably be contended that this greater average age of the male parent was the cause of the excessive production of male offspring in the cross matings. To make such a contention, however, would simply be to affirm belief in Sadler's "law" [1] or some variant of it which holds that the relative age of the parents is causally related to the sex-ratio of the offspring. In regard to this matter it need only be said that Sadler's theory has been abandoned by all recent students (both from the biological and from the demographic side) of the problem of sex simply for the reason that nothing remotely approaching conclusive evidence has ever been brought forward in its support.

4. That the individuals in the cross mating are exposed to environmental influences different on the average from those acting on the individuals in pure matings and that the differences in the sex-ratios of the offspring of these two groups are the result of these environmental differences. This possible explanation obviously needs careful consideration. So far as broad environ-

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[1] *Cf.* Geddes and Thomson, "The Evolution of Sex" or any of the standard works on vital statistics for an account of this law.

mental factors such as climate are concerned there can be no dif-
ferential effect on the sex-ratio for the two groups since all the
statistics are derived from the population of a single city. In a
general sense all the individuals live in the same environment.
But there is a possibility of a difference between the different
groups in regard to the complex of environmental factors which
are collectively implied in "social status." It is conceivable that
on the average the Italian-Argentine families are of different social
status than Italian-Italian or Argentine-Argentine families in the
same city. Differences in social status imply differences in nutri-
tion, in housing and in other physical conditions of existence.
Some one or all of these things might conceivably be held to
affect the sex-ratio in the manner observed. In considering this
point it needs to be held clearly in mind that there are two dis-
tinct questions involved. These are : (a) Is there any conclusive
evidence that there does exist as a matter of fact any uniform
average difference in the social status of individuals in cross as
compared with pure matings ? And (b) granting that such an
average difference does exist what evidence is there that it would
produce the observed effect on the sex-ratio ? To the first of
these questions it is difficult to get any answer. Careful study
of all the available demographic statistics of Buénos Ayres has
failed to yield any conclusive evidence on the point. The prob-
ability appears to be, however, that if any difference at all exists
in the social status of the two groups it is in the long run (or on
the average) not marked in degree. Further it appears probable
that whatever difference does exist is in the direction of a lower
social status in the case of the cross matings.

Regarding the influence of such a difference (if it exists) on the
sex-ratio it seems probable that it would have very little or no
effect. Punnett [1] has recently made a very careful study of just
this point for certain elements of the population of London. He
finds that in the classes of lower social status more females than
males are born, and *vice versa*, but concludes in general that pa-
rental nutrition has no sensible influence on the sex-ratio. Mor-
gan [2] reviews the literature on the subject and reaches the fol-

[1] Punnett, R. C., "On Nutrition and Sex Determination in Man," *Proc. Camb. Phil. Soc.*, Vol. 12, 1903.

[2] Morgan, T. H., "Experimental Zoölogy," New York, 1907, pp. xii + 454.

lowing conclusion (p. 385) : "If nutrition were really a factor of any importance in sex determination, it is surprising to find so little difference under apparently very favorable and unfavorable conditions. It seems much more probable that if the nutrition affects in any way the proportion of the sexes, it does so indirectly by elimination, and not by determining either the sex of the embryo or of the egg." Further on Morgan says in discussing Geddes and Thomson's theory of sex (p. 388) : "If, on the other hand, the determination of sex is supposed to be due to the nourishment of the embryo, the best ascertained facts, both experimental and statistical, are opposed to the hypothesis." Taking all these points into consideration it seems very doubtful, to say the least, if the observed excess of males in the cross matings has its explanation either in whole or in part in differences in the environmental complex implied by " social status." However, in the absence of more complete and definite statistical data regarding the point one cannot be dogmatic in asserting such a conclusion.

If none of the suggested factors can reasonably be held to afford an explanation of the facts regarding the sex-ratio shown by the present statistics how are these facts to be interpreted ? All that can safely be asserted is that the present statistics, within their limits, show clearly that there is a definite relation between the character of the mating and the magnitude of the sex-ratio. Is this a *post hoc* or a *propter hoc* relation ? The data themselves do not *conclusively* demonstrate which it is. Nor does it seem probable that statistics of human births alone can ever settle this question. It is one which demands experimental analysis. The chief difficulty involved in maintaining that there is a causal relation between the character of the mating and the sex-ratio lies in the lack of knowledge as to what could be the physiological mechanism by which the causation was effected. In a way the phenomenon appears somewhat analogous to the well-known phenomenon of xenia observed in plant breeding, differing in that here the character influenced is sex rather than some purely morphological feature of the organism.

In conclusion it should be said that the data presented in this paper are not put forth as in any way final or conclusive. They

require confirmation from other sources and *experimental* analy-
sis.   Within their limits, they lead to a definite and significant
conclusion as to fact.   In so far they contribute to the discussion
of the general problem of determination of sex.

SUMMARY.

   Statistics of over 200,000 human births extending over a pe-
riod of 10 years in the city of Buénos Ayres show that the pro-
portion of males to females is significantly greater when the
parents are of different racial stocks than when they are of the
same.   In the data are involved three racial stocks in pure and
cross matings.   The preponderance of males in the offspring of
cross matings appears not to be capable of explanation as the
result of environmental or demographic influences.   Experimen-
tal investigations are necessary in order to reach adequate
explanations of such statistical facts regarding sex ratios as are
set forth in this paper.

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BIOLOGICAL BULLETIN

A SIGNIFICANT CASE OF HERMAPHRODITISM IN FISH.[1]

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The subject of hermaphroditism in fish has received the attention of only a few workers. Our principal information is derived from the work of Stephan ('01). This author describes for certain species of fish a complete and simultaneous hermaphroditism, ripe ova and spermatozoa appearing in the same individual at the same time ; for other species a protandric hermaphroditism, the individuals while young being males and later in life becoming females ; for still others, a precocious appearance of sexuality in the males and a tardy appearance of the latter in the females of species still considered as unisexual.

The condition last mentioned is interpreted by Roule ('02), on the basis of rather doubtful evidence, as a true case of protandric hermaphroditism. He measured large numbers of sexually mature individuals belonging to several species of Cyprinidæ, and found that all of the individuals of small size were males and all those of large size were females. Hence, according to Roule, all individuals are males when young and females when older. The only alternative interpretation of the facts presented seems to be that these species exhibit strict unisexuality of all individuals, with dwarfing of the males and precocious appearance of male sexuality. Roule points out, however, that, on this basis, one would expect to find among the smaller individuals young females with immature sex glands, and that there should be at least as many of the latter as there are adult females. But none such were found by him.

[1] Contribution from the Zoölogical Laboratory of the University of Texas, No. 94.

Roule's paper, being simply a preliminary statement, is too inadequate to furnish the basis for a detailed discussion, yet it might be well to point out that the Pœciliidæ, a family rather closely related to the Cyprinidæ with which Roule worked and about which there can be no suspicion of normal hermaphroditism, exhibit conditions closely parallel to those cited by Roule.

Let us take, for example, the state of affairs in *Fundulus majalis*. Here the mature males are, on the average, considerably smaller than the mature females; yet the largest of the males often surpass in size the smaller sized females. Again, the very smallest sexually mature individuals are always males and the very largest are always females. The males also mature distinctly earlier in the season than do the females. All of these facts attest the precocity and dwarfing of the males.

In view of the fact, however, that in *F. majalis* there is a very pronounced sexual dimorphism that begins to make itself apparent in very young and immature fish, it becomes certain that all individuals are unisexual throughout life. The individual whose discovery gave occasion for this paper, is the only exception to this rule that has come under the observation of the writer although he has examined thousands of specimens of this and allied species during the last three years.

In order that the reader may more readily understand the account of this rather remarkable case of hermaphroditism it seems necessary to recapitulate certain facts concerning the sexual dimorphism and spawning behavior of *Fundulus majalis*, a subject treated extensively in former papers (Newman, '07 and '08).

In *F. majalis* the sexes differ in the following particulars :

1. The females are larger, on the average, than the males.

2. The body color pattern of the two sexes is entirely different; that of the male consisting of distinct transverse bands running from back of the head to near the base of the caudal fin (see Fig. 1); that of the female, on the other hand, consisting essentially of well-marked longitudinal stripes, perfect anteriorly and merging posteriorly into a few cross bands like those of the male (see Fig. 4).

3. The cross-banded pattern is the primitive one for the family as well as for the species, and all young fish of both sexes start out with this pattern. The males retain this juvenile pattern, in a somewhat strengthened form, throughout adult life. In the females, however, the primitive cross-banded pattern is gradually transformed into one characterized by longitudinal stripes, in the following manner. The cross bands, beginning with the anterior ones, show thickenings in two places. The parts of the bars between these thickened regions thin out and disappear, leaving
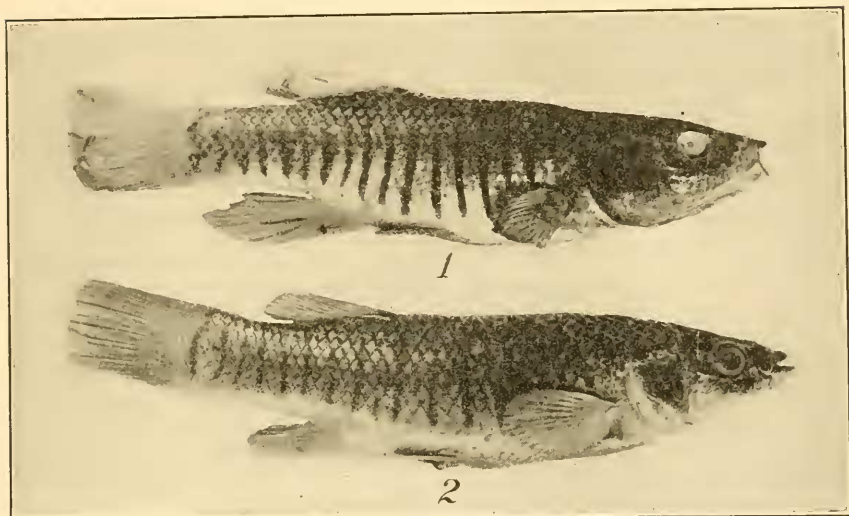
FIG. 1. Photograph of preserved specimen of male *Fundulus majalis* from the right side (slightly reduced). This specimen shows the dark spawning coloration about head and back, the large size of dorsal and anal fins, the typical cross-banded pattern. The characteristic male marking on the dorsal fin, however, shows only faintly.

FIG. 2. Photograph of the hermaphrodite specimen of *F. majalis*, taken with the same exposure as Fig. 1. Note that the general body coloration is almost that of the male, but that the cross-banded pattern is weaker. This pattern, however, was much stronger in life. In other respects it resembles the female (Fig. 4).

the thickened regions arranged in two rows. These then fuse longitudinally into two or more stripes. This process is described fully and figured in a former paper (Newman, '07).

4. The male is characterized by the presence of a very prominent dark spot or series of spots, surrounded by a light area situated on the posterior rays of the dorsal fin. The photograph

(Fig. 1) does not do this character justice. A far better idea of the prominence of this sexual marking can be obtained from an examination of the illustration in the paper just referred to.

5. The dorsal and anal fins of the male are much larger and stronger than those of the female and are used as clasping organs in spawning.

6. These fins and all parts of the body of the male that come into intimate contact with that of the female in spawning and courtship are covered with small finger-like papillæ that lend to these parts a decided roughness and undoubtedly assist the male in holding the female securely. These organs have elsewhere been designated "contact organs."

7. During the sexual climax the whole body of the male is suffused with dark pigment, some specimens showing an almost inky blackness on head, cheeks and back. The female, however, retains her normal pale olivaceous tint, or in many cases becomes distinctly paler than during the vegetative season.

8. The flesh of the female, during the height of the spawning season, becomes softer than usual and the abdomen is greatly distended with ripe ova.

9. The behavior of the males, during the spawning season, is sharply contrasted with that of the females. The former are spirited and pugnacious, and frequently follow the females about in order to spawn with them. Actual spawning, however, was observed only occasionally in *F. majalis*, but it is essentially like that of *F. heteroclitus*, which was observed hundreds of times. The behavior of the female is characteristically coy.

These and a few minor differences between the sexes will serve to render intelligible the account of the individual now to be described.

Description of the Hermaphrodite Specimen.

The fish herein described was discovered by merest chance during the progress of some breeding experiments at the Woods Hole laboratories.

On July 3, 1907, needing a male *Fundulus majalis*, I rather hurriedly dipped out of the aquarium what I took to be a large, but decidedly pale, male. Wishing to perform an experiment

with the milt of just such a male as this seemed to be, I attempted, without further examination, to strip milt from the specimen. Instead of milt a stream of eggs issued from the short genital tube at the base of the anal fin. I knew, of course, that fish frequently eat eggs and pass them undigested through the digestive tract, but such eggs are always dead and opaque, while these eggs were normally transparent. Surprised at the extrusion of eggs from an individual supposedly male I proceeded to make a careful examination. This revealed the fact that the fish was male only in one respect. It showed the cross-banded body pattern of the male very distinctly. It lacked, however, the characteristic spot on the dorsal fin, the large size of dorsal and anal fins, contact organs, and intensified pigment of the typical male ; while it possessed the distended abdomen soft flesh, lighter ground color, small fins, and external oviducal tube of the spawning female. Yet I had never before seen an adult or even a juvenile female without longitudinal stripes distinctly indicated.

The specimen seemed sufficiently unusual to deserve a separate aquarium, where it was well fed and relieved of its burden of eggs several times during the ensuing fortnight. These eggs showed a rather low degree of fertility, although at least ten per cent. developed in each case.

After about a week a typically marked female of about the same size was introduced into the special aquarium for the sake of comparison, and both normal and abnormal specimens were treated alike. For nearly two weeks the two fish behaved alike, but after that time the cross-banded fish began to lose its quiet passive behavior and to assume a decidedly overbearing attitude toward its companion. Several of my fellow investigators called my attention to this curious behavior, which might well be termed "bossy." Accompanying this change in behavior were several morphological changes. The body became slimmer, as would be expected since the eggs had practically all been extruded, the flesh became harder, and dark pigment was laid down all over the body. The latter was most noticeable on head and cheeks which had become decidedly dusky, a change very characteristic of males entering upon the period of high sexual tone. The cross bands become darker and more distinct and a faint wash of orange tint appeared on the anal fin, a distinctly male character.

During the last week of July the fish was kept under close observation. On several occasions it showed a type of behavior distinctly male-like. It followed the female about and repeatedly made movements that seemed to indicate a weak attempt at spawning. Of this I could not be positive, but in other respects the behavior was that of a courting male. It would have surprised me greatly had there been an exhibition of actual spawning, for, as has been said, *F. majalis* seldom spawns in captivity.

On the last day of July the writer was compelled to leave the laboratories and the fish was killed and carefully preserved in formalin.

An examination of the formalin-preserved sex gland revealed the fact that it was a composite gland, containing about five per cent. of testicular tissue, slightly immature, and imbedded in a mass of immature and stale ovarian tissue. The testicular tissue occurred in minute lumps, principally near the posterior end of the gland. Although distinctly testicular in structure, these small masses showed a less typical structure than that of normal testis, being less compact and interspersed with connective tissue. The color, size and general appearance of the whole gland was that of a preserved testis, there being no yellow color present as is the case in normal ovaries after the close of the spawning season.

A further close examination of the body pattern showed that the cross banding on right and left sides was not equally perfect, that of the right side showing the character in as perfect a form, if less distinct, as in a typical male, that of the left being partially broken into shorter bars, the beginning of a tendency on the part of the cross-banded pattern to break up into the rows of spots that furnish the material for longitudinal stripes.

The photograph of the specimen taken from the right side shows the pattern far less distinctly than in life on account of the fact that scales and skin, rendered opaque by the preservative, obscure the underlying markings. In other respects the illustration (Fig. 2) is a faithful representation of the conditions. Photographs of the left side failed entirely to bring out the points desired, so it was necessary to insert a camera drawing as the best substitute. This drawing (Fig. 3), showing the less perfect

cross banding, when compared with the average condition seen
in an adult female (Fig. 4), will show a striking contrast.   It
will be noted that the hermaphrodite exhibits a somewhat juve-
nile figure in that the head is shorter, the body broader and the
tail less tapering.   These points might not be patent to one not
very familiar with the species.
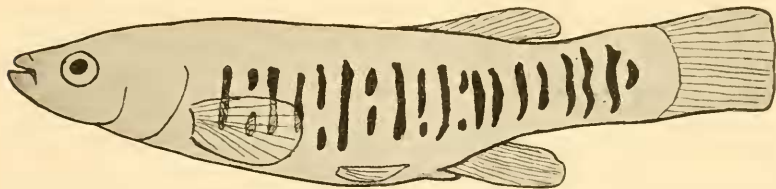
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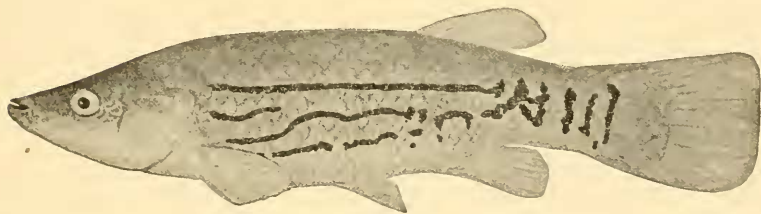
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FIG. 3.   Outline camera drawing of the hermaphrodite from the left side, to show
the rather broken character of the cross-banded pattern.

FIG. 4.   Wash drawing, showing a typical female *F. majalis*.   Many specimens
show a far more complete transformation of the juvenile cross-banded pattern into the
series of longitudinal stripes but few females of this size show a less advanced con-
dition.   Note the long head, comparatively small dorsal and anal fins, and compar-
atively light ground color of head and back.

General Considerations.

1. The extreme rarity of hermaphroditism in fish normally
unisexual makes this case worthy of note, especially as the sexes
are so well differentiated in form, color pattern, and behavior.
·No other case comparable with this is on record.   There seems,
in fact to be only one case of abnormal hermaphroditism in fish
in the available literature.   This is a brief description by South-
well ('02), of a hermaphrodite gland taken from a smoked her-

ring. The only point of interest for this discussion, since herrings seem to show no sexual dimorphism, is that the testicular tissue was located posterior to the ovarian tissue and overlapped the latter somewhat. This condition of the sex glands reminds one of the composite gland described in the preceding paragraphs.

2. Some light is thrown on the influence of the sexual secretions upon the secondary sexual characters. In this case the presence of a comparatively minute amount of imperfect testicular tissue has had the negative effect of inhibiting, in an individual predominantly female, the transformation of the juvenile into the female color pattern ; and the positive effect of producing in this individual, at the expiration of the season's period of egg production, an approximation of male coloration and behavior.

3. In all cases of serial hermaphroditism described in available literature the hermaphroditism is protandric and in successive seasons. Here the sequence was distinctly protogynic and the changes occurred within a period of less than a month. The condition is decidedly anomalous.

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THE HOMING OF THE MUD–DAUBER.

C. H. TURNER.

INTRODUCTION.

In my paper on " The Homing of Ants "[1] there is recorded evidence that ants find the way home neither by a homing instinct nor by reflex action nor merely by kinesthetic responses ; but by utilizing landmarks. In this paper I propose to record experimental evidence that the same is true of the common mud-dauber wasps.

It has long been recorded by keen observers that both the social and the solitary wasps, on leaving their nests for the first time, carefully examine the surroundings before flying away. It is also stated by some that any alteration in the immediate surroundings of the nest will render it difficult, or even impossible, for the wasp to find its way back again.

Mr. and Mrs. Peckham, who have devoted much time to the study of both the social and the solitary wasps, say :[2] " If they were furnished with an innate sense of direction they would not need to make a study of the locality of the nest in order to find the way back, but if they were without this sense it would be only common prudence to take a good account of their bearings before going far afield. . . . In reading much of the popular natural history of the day one might suppose that the insects seen flying about on a summer's day were a part of some great throng which is ever moving onward, those that are here today being replaced by a new set tomorrow. Except during certain seasons the exact opposite is true. The flying things about us abide in the same locality and are the inhabitants of a fairly restricted area. The garden in which we worked was, to a large extent, the home of a limited number of certain species of wasps that had resided there from birth or, having found the place accidentally, had settled

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[1] *Jour. of Comp. Neur. and Psy.*, Vol. XVII., pp. 367–434, Pl. II.–IV.

[2] G. W. and E. G. Peckham, " On the Instincts and Habits of the Solitary Wasps," Madison, Wis., 1898, pp. 212, 213, 215.

there permanently. . . . After days passed in flying about the garden
— going up Bean Street and down Onion Avenue, time and again
— one would think that any formal study of the precise locality
of a nest might be omitted, but it was not so with our wasps.
They made repeated and detailed studies of the surroundings of
their nests. Moreover, when their prey was laid down for a
moment on the way home, they felt the necessity of noting the
place carefully before leaving it. . . . If the examination of the
objects about the nest makes no impression upon the wasp, or if
it is not remembered, she ought not to be inconvenienced nor
thrown off her track when weeds and stones are removed and the
surface of the ground is smoothed over ; but this is just what
happens. *Aporus fasciatus* entirely lost her way when we broke
off the leaf that covered her nest, but found it, without trouble,
when the missing object was replaced. All the species of *Cer-
ceris* were extremely annoyed if we placed any new object near
their nesting-places. Our *Ammophila* refused to make use of
her burrow after we had drawn some deep lines in the dust before
it. The same annoyance is exhibited when there is any change
made near the spot upon which the prey of the wasp, whatever it
may be, is placed. We learned from experience how important it
was not to disarrange the grass or plants on such occasions.''

All this was written before Bethe [1] had restated, with emphasis,
his theory that bees (the morphological and physiological kinship
of which to wasps leads one to expect them to be psychologically
similar) are guided home by an unknown force ; and before
Pieron [2] had asserted that ants are led home by a reflex kines-
thetic sense. This being the state of affairs a crucial experiment
seemed to be needed. The mud-dauber (*Sceliphron*, Klug =
Pelopœus, Latr.) was selected, partly because its habits rendered
it comparatively easy to obtain material and partly because, so
far as I know, no such experiments have been performed upon it.

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[1] A. Bethe, '' Die Heimkehrfähigkeit der Ameisen u. Bienen zum Theil nach neuen
Versuchen,'' *Biol. Centrlbl.*, 2 Bd. (1902), no. 7, pp. 193–215 ; no. 8, pp. 234–238.
[2] H. Pieron, '' Du rôle sense musculaire dans l'orientation des fourmis,'' *Bull.
Inst. Gen. Psy. Paris*, T. 4 (1904), pp. 168–187.

Preliminary Observations.

These preliminary observations were made in a laboratory the walls of which were ceiled with tongue-and-grooved pine boards. These boards were arranged vertically. Two of the walls were supplied with windows and two were not. Near the top of each of these walls mud-daubers constructed nests. Some of these nests were in dark places and some were in light places. I noticed that the wasp never flew directly to the nest, but that it would alight on a certain crack. After ascending, afoot, this crack, until it had reached the height of the nest, it would turn and walk to it. The same wasp always alighted on the same crack and at about the same distance from the floor. This led me to suppose that wasps used the cracks as landmarks. In this room a certain window was lowered from the top, through which opening the wasps came and departed. In another room, in which similar experiments were conducted, the window was raised from the bottom. Wasps frequented this room as much as they did the other. Evidently wasps can learn the way into a room by either a high or a low opening.

The Environment of the Experiments.

This series of experiments was performed in a laboratory thirty-seven and a half feet long, twenty-five feet wide and twelve feet
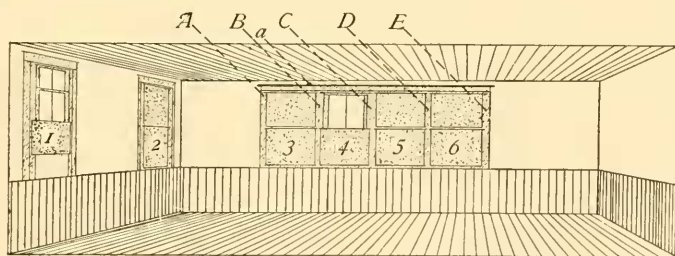
Fig. 1. This is a diagram of the room arranged for experiment one. 1–6, windows; *A–E*, upright facings of windows; *a*, location of the nest. The wood-work of the windows is shaded with broken lines, the window-shades with dots. The boards in the floor, ceiling and dado are drawn twice as wide as they were.

high (Fig. 1) which was situated in the third story of a large brick building. The ceiling was covered with tongue-and-grooved pine boards and a four-foot dado of pine ceiling extended around

the lower third of the walls of the room.   Excepting the space
occupied by windows, doors and dado, the walls were plastered
in the rough.   In the west wall there were two windows (Fig. 1, 1
and 2); in the north, four (Fig. 1, 3 to 6).   The windows of the
north wall were close together, being separated by wooden par-
titions only one foot wide (Fig. 1, B, C, D).   Across the top of
each window there was a piece of three inch moulding.   On the
north wall this moulding extended continuously across the four
windows.   There were two green blinds to each window, one to
each sash.   These blinds were not quite opaque.   The ceiling
was painted green ; the walls, including dado, doors and window-
facings, cream color.

In order to have only one entrance for the wasps, the lower
sash of window number one was raised half way.   All other
windows were closed.   This condition was maintained through-
out the entire series of experiments.   To furnish definite light
relations for the beginning of the experiment, the lower shade of
window number one was raised about half way and the top
shades of windows one and three raised as far as possible.   All
the other shades were down.   After these conditions had been
maintained for nearly two weeks a mud-dauber began the con-
struction of a nest on the moulding above window number three
at a point about six inches from upright B (Fig. 1, a).

When first discovered the wasp had completed nearly half of
one cell ; hence it had already made several trips back and forth
through window number one.   I watched the wasp make several
trips, and each time it behaved as follows.   On entering the
room it would fly obliquely upwards to the upper third of upright
B.   Then it would fly vertically upwards almost to the ceiling,
thence it would fly leftward to the nest.   The line of flight from
the entrance to upright B was perceptibly curved, the convexity
being towards the east.   The flight from the entrance through
window number one to the nest consumed about half a minute.
In departing, the wasp flew downwards in a curve from the nest
to the upper portion of the opening through which it had entered
the room.   After watching the wasp make several trips in
practically the same manner, the following experiments were
performed :

EXPERIMENT 1.

The lower shade of window number one was raised half way and the top shade as far as it would go. While the wasp was out of the room, all the blinds of windows number two to six were closed except the upper shade of window number four, which was raised as far as possible (Fig. 1).

The wasp on entering through window number one flew obliquely upwards across the beam of light from window number four to the upper third of upright C. (This line of flight was convex towards the east.) It then flew vertically upwards almost to the ceiling then leftward about a foot (this is a little more than the distance of the nest from upright B) and examined carefully the moulding. Not finding the nest, it began flying first to the right and then to the left in constantly elongating ellipses with very short minor axes. All this time it was carefully examining the moulding. Occasionally the mud-dauber would fly downward into the beam of light and then resume its search. In its lateral flights the wasp sometimes flew as far to the east as upright D and to the west almost as far as upright B. At the end of three minutes it had not found the nest, although under former conditions of illumination it required only half a minute to fly from window number one to the nest.

While the wasp was still searching for the nest, the top shade of window number four was lowered and the corresponding shade of window number three raised as far as possible. This reproduced the conditions under which the wasp had originally worked.

Almost immediately the wasp found the nest !

EXPERIMENT 2.

The lower shade of window number one was raised half way and the top shade as far as possible. While the wasp was out of doors, all the shades of windows number two to six were lowered except the top shade of window number five, which was raised as high as possible.

On entering, the wasp flew in a fairly direct line towards the nest. When about one third of the way across the room, it returned almost to window number one and described a circle of about a foot in diameter. It then flew to the middle of the upper

shade of window number four. Thence it flew upwards almost to the ceiling and then leftward to the nest.

EXPERIMENT 3.

The lower shade of window number one was raised half way and the upper shade as far as possible. All of the shades of windows number two to six were lowered except the top shade of window number three, which was raised as far as possible. This reproduced the conditions under which the wasp had worked originally.

On entering the room the wasp flew obliquely upwards to the upper third of upright B. Then it flew vertically upwards almost to the ceiling. Thence it flew leftward to the nest. The line of flight from the entrance to upright B was perceptibly curved, the convexity extending towards the east. The total flight from the entrance to the nest consumed about half a minute. The shades were maintained in the above position until the mud-dauber had made three trips. Each was made in practically the same manner.

EXPERIMENT 4.

The same conditions as in experiment one.

The behavior was practically the same as in experiment one. In this experiment, however, the shades were maintained in the same position until the wasp had found the nest, which required nearly five minutes.

The wasp was allowed to make two trips. Its behavior on the second trip resembled that on the first ; but it required only three minutes to pass from the entrance to the nest.

EXPERIMENT 5.

The same conditions as in experiment three.

The wasp behaved the same as in experiment three.

EXPERIMENT 6.

The lower shade of window number one was raised half way and the top shade as high as possible. All of the shades of windows two to six were lowered, except the top shade of window number two, which was raised as far as possible.

The wasp on entering the room described a small circle then

flew obliquely upwards to a point almost to the ceiling, but a little to the west of upright *A*. It then flew alternately leftward and rightward until the nest was found, which consumed about one minute.

The wasp was allowed to make two trips. Its behavior on the second trip was similiar to that on the first, and about the same amount of time was consumed in passing from the entrance to the nest.

Experiment 7.

The conditions were the same as in experiments three and five.

The wasp was permitted to make two trips. It behaved the same as it did in experiments three and five.

Experiment 8.

The lower shade of window number one was raised half way and the top shade as high as possible. All the shades of windows two to four were lowered.

On entering the room the wasp described several small circles. It then flew first to about the middle of the upper sash of window number three, then to window number two, then to window number five. Finally, after much searching, the nest was found.

The shades were retained in the above condition until the wasp had made two trips. On the second trip it went first to upright *C* and then, after a short search, it found the nest.

Experiment 9.

The same conditions as in experiments three, five and seven.

The behavior was the same as in experiments three, five and seven. Two trips were made.

Experiment 10.

At first the conditions were the same as in experiment eight. While the wasp was on the nest, the top shade of window number one was lowered.

On leaving the nest the wasp flew away through the window in its usual way. The lowering of the top shade of window *A* did not change its behavior.

Experiment 11.

The lower shade of window number one was raised half way and the top shade lowered. While the wasp was out of doors, all the shades of windows two to six were lowered except the top shade of window three, which was raised as high as possible.

The wasp behaved the same as in experiments three, five, seven and nine.

Experiment 12.

The lower shade of window number one was raised half way. While the wasp was out of doors, all of the other shades were lowered.

The wasp behaved the same as in experiment eight.

Experiment 13.

The lower shade of window number one was raised about half way. While the wasp was out of doors, all the shades of windows two to six were lowered except the lower shade of window number three, which was raised as far as possible.

At first the wasp searched carefully the upper portion of the wall to the west of the upright *A*. Then, as a result of extending its search to the east, the nest was discovered.

This experiment was repeated with the same results.

Experiment 14.

The same conditions as in experiments three, five, seven, nine and eleven.

The wasp behaved the same as it did in experiments three, five, seven, nine and eleven.

Experiment 15.

The same conditions as in experiment one.

The wasp behaved as in experiment one. It took about one minute to find the nest. The wasp was allowed to make two trips.

Experiment 16.

The same conditions as in experiment one.

After the shades had been maintained in this position for about two days, the wasp on entering the room flew obliquely upwards

to near the top of upright C and then obliquely leftward and upwards to the nest.   The trip from window number one to the nest consumed much less than a minute.

EXPERIMENT 17.[1]

The same conditions as in experiment three.   This experiment was performed immediately after the close of experiment sixteen.

The wasp on entering the room flew obliquely upwards, across window number four, to the upper third of upright C; then obliquely leftward and upwards, across windows number four and three, to a little beyond the upright A.   It then searched about until the nest was found.

The shades were left in this condition from 10:45 A. M. July 19 to 9 A. M. July 20, at which time the wasp occasionally visited the nest.   The wasp on entering the room, flew obliquely upwards, across window number three, to the upper third of upright B; then leftward, across window number three, to a little beyond upright A, then obliquely rightward and upwards to the nest.   The conditions in this experiment and in experiments three, five, seven, nine and eleven are identical, yet the behavior in this case is quite unlike what it was in those.   Evidently prolonged exposure to the conditions described in experiment sixteen has modified the behavior of the wasp.   It had lost (forgotten) its old response to the conditions described in experiment three and been forced to acquire a new response.

CONCLUSIONS.

From these experiments it is evident that, in finding its way back to its nest, the mud-dauber is guided neither by what is known as a homing instinct nor by what Pieron has called a kinesthetic reflex ; for if either assumption were true, a manipulation of the light should not have altered the wasp's behavior.

Evidently light plays a prominent rôle in the homing of wasps, yet the behavior of the mud-dauber is not a phototropism ; for in

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[1] This series of experiments was begun on the morning of July 17, 1908, and ended on the morning of July 20, 1908.   Experiments one to fifteen inclusive were performed the first day and in the order mentioned.   The intervals between the experiments were only sufficiently long to permit the necessary adjustments to be made.   Between experiments fifteen and sixteen there was an intermission of almost two days ; between experiments sixteen and seventeen, an intermission of five minutes.

no case did the wasp so orient itself as to have the major axis of its body parallel to the rays of light. Furthermore in hunting for the nest, the wasp crossed the light sometimes in one direction and sometimes in another. In yet other cases the wasp would zigzag across the light.

Neither is the wasp's behavior merely a reflex response either to brightness or to the direction of the rays of light; for if that were the case, in experiment six, when all the shades of windows number two to four were lowered except the top shade of window number two, the wasp should have flown, not to the wall to the west of window number three, but to window number two. Likewise in experiment eight, when all the shades of windows number two to six were lowered and the only bright light entering the room was that which came through the upper and lower portions of window number one, if the wasp were guided merely by light acting reflexly, then it should not have been able to find the nest at all. Furthermore, if the wasp's behavior is merely a reflex response to light, there is no reason why it should have entered the room at all, for the open portion of the window was certainly not so bright as the window-panes from which the light was reflected. We say nothing about the bright sunshine out of doors !

But brightness is not the only factor which influences the movements of this wasp; else, when all the shades of windows number two to six were lowered, it would have been impossible for it to rediscover the nest. This series of experiments warrants the induction that, in the wasp's memory, that nest is located in a certain direction and at about a definite distance from a bright patch which is situated at a known elevation in a peculiar environment.

The above statement predicates to wasps memory and an awareness of space relations. As to the existence of memory these experiments furnish unequivocal evidence. This harmonizes with the views of Forel and the Peckhams. In " The Homing of Ants " are recorded proofs that ants have an awareness of space relations, and, since wasps are near kin to ants, it is probable that they, too, have an awareness of space relations. This series of experiments furnishes evidence to support this view. In

almost every experiment of this series the lower shade of window number one was raised half way and the top curtain all of the way. This was done in order to have the departing wasp confronted, on each trip, by an upper and a lower bright patch.   Were the wasp responding to a bright patch merely and not to a bright patch in a definite place, then the wasp should have flown to the upper bright patch just about as often as it did to the lower.   The wasp always flew directly from the nest to the opening in window number one!   There was but one exception to this statement.   On one occasion I was standing on a ladder watching the wasp construct the nest.   I was within two feet of the nest.   On that occasion the wasp, on departing, circled about once or twice and then returned to the nest and from there flew to the exit.

In brief, these experiments warrant the conclusion that the flying mud-dauber, like the creeping ant, is guided by certain landmarks, and that light plays a prominent rôle in furnishing such landmarks.

HAINES NORMAL SCHOOL,
    AUGUSTA, GA., July 25, 1908.

EXTRUSION OF THE WINTER EGG CAPSULE IN PLANARIA SIMPLISSISSIMA.[1]

FLOYD E. CHIDESTER,

FELLOW IN ANATOMY, THE UNIVERSITY OF CHICAGO.

About the middle of October, 1907, I chanced to note that some of the *Planaria simplississima* in one of my aquaria had developed egg capsules.

I immediately transferred a number of flatworms, including those that had already formed capsules, and a few that had not as yet developed them, to a small aquarium on my desk. While examining one of the planarians and its capsule under the microscope, I saw the movements connected with the extrusion of the capsule.

When first observed, the capsule lay lengthwise of the body in the position indicated in Fig. 1.

Presently the capsule was turned by the movement of the body of the worm until it occupied a position as indicated in Fig. 2,

FIG. 1.   FIG. 2.   FIG. 3.

then slowly came to the position indicated by Fig. 3, that is, at right angles to the longitudinal axis of the body.

This change in position necessarily increased the size of the cavity in which the capsule lay, lacerating the tissue and permitting easy egress.

[1] Contributions from the Biological Laboratory, Clark University.

The planarian then moved slowly forward, the capsule passing along through its body and out at the dorsal caudad region. The rotation of the capsule in the body of the animal apparently aided in breaking the wall of the cavity in which the capsule lay, for there seemed to be no difficulty in the passage through the posterior portion of the body and out near the tail (Fig. 4).

The entire process of extrusion occupied only about thirty minutes.

The next day the wound where the capsule had originally lain was partly closed by contraction of the surrounding tissue, and the wound in the tail region made at the escape of the capsule was obliterated almost entirely.

I was interested to see if the same planarian forms more than

Fig. 4.
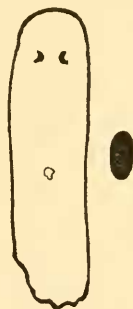
Fig. 5.

one egg capsule, so isolated the animal I had been observing, and examined it several times each day.

In a week complete regeneration was effected. At the end of twenty days from the time I had seen the first capsule, another appeared, evidently formed during the night, and I had the good fortune to observe its extrusion also. The movements were the same as before observed, except that the capsule was extruded on the right side of the body this time.

Other planarians bearing capsules were observed, and in all cases the capsule was rotated immediately before the extrusion

The individual described previously, at the end of about three weeks more, extruded a third capsule.

Kept in a small vial on my desk for two months after this extrusion, the planarian formed no more capsules.

The winter egg capsule of *Planaria simplississima* is a dark brown, elongated object, with a horny covering. It bears nothing so far as I could discover that would aid in holding it fast. Several capsules were opened carefully by means of sharp needles and the contents examined. There were perhaps a score of eggs and many nutritive cells.

Summary.

1. *Planaria simplississima* produces winter eggs.

2. A single individual may develop three or more capsules during the winter.

3. Complete regeneration of tissue lacerated at the extrusion of the egg capsule is effected in about one week.

4. About three weeks elapse between two successive extrusions.

LYSOROPHUS, A PERMIAN URODELE.

S. W. WILLISTON,

University of Chicago.

Thirty-one years ago Professor Cope described [1] briefly three small and incomplete vertebræ from the " Permian " of Vermilion County, Illinois, as those of a reptile under the name *Lysorophus tricarinatus.* The type specimen was figured, with additional descriptions, by Case in 1899.[2] In a later paper [3] Case recognized the same form from the Permian of Texas and gave a good description and figures of the vertebræ and ribs. From the peculiar coiled condition of the various intermingled series of vertebræ which he had himself collected he concluded that the animal was long and snake-like. No limb or pectoral or pelvic bones have ever been detected. Associated with the form but not definitely connected with the vertebræ was a fragment of the skull of a small animal which he doubtfully referred to the same species, but which he also was inclined to refer to *Isodectes* Cope. In 1904 Broili [4] with real skull material and less perfect vertebræ, reached the startling conclusion that the genus showed certain affinities to the fishes, because of the presence of what he thought were gular plates in the palatine region. Chiefly because of their supposed presence he proposed the family name Paterosauridæ for the genus, which he located in the Rhynchocephalia. It is needless to say that his views of the diphylectic origin of reptiles, one phylum directly from the fishes, the others from the amphibians, has been received by naturalists with doubt and incredulity, and are, as will be seen, wholly unsubstantiated by this animal. His "gular plates" were doubtless merely misplaced proatlas bones. It is rather surprising that he should have overlooked the almost impossible reptilian char-

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[1] *Proc. Amer. Phil. Soc.*, 1877, p. 187.
[2] *Journal of Geology*, V., p. 714, pl. II., ff. 12a, 12b, 12c.
[3] *Ibid.*, May, 1892, p. 46, pl. IX., ff. 1, 2.
[4] *Paleontographica*, LI.

acters of the vertebræ and skull, characters certainly impossible for a rhynchocephalian.

Recently, in examining the material in the Chicago collections, the remarkable characters of the vertebræ, so anomalous for any reptile, and utterly unknown in this class from the Permian otherwise, aroused my interest and doubt. From the matrix containing several series of vertebræ a corner of a bone protruded which I recognized as of a mandible. Under the skilful manipulations of Mr. Paul Miller a wonderfully complete and undistorted skull was brought to light. In similar matrix, and associated with vertebræ of the same kind I recognized another mandible and several small, pitted dermal bones, probably belonging to another type of amphibian, though it is not impossible the scutes were those of *Lysorophus*.

That the present species belongs in the genus *Lysorophus* from the reputed Permian of Illinois seems tolerably well assured, though the type material of the genus is rather scanty, and not entirely sufficient to resolve doubt. That the species are identical is I believe quite improbable. With this understanding, however, it will do no harm to use Cope's name for both genus and species until such time as more and better material of the species has been obtained from the original or contemporaneous beds.

Lysorophus tricarinatus Cope.

Skull (Figs. 1–3). — The general shape of the skull is that of a four-sided pyramid, pointed anteriorly. The upper surface is nearly plane, very gently convex from side to side, and also longitudinally in front. The sutures are widely separated in the specimen, indicating a loosely joined skull, and the bones are quite smooth, without pittings or mucous canals. The nasals are relatively large bones, with nearly parallel sides, rounded anteriorly. The frontals are also four-sided, the longer sides nearly parallel ; the bone is about twice as long as wide. On either side, beginning at the transversely extended fronto-parietal suture, there is a narrow bone which seems to be continuous as a single element to beyond the middle of the nasals, ending acuminately in front. This is doubtless the prefrontal of the modern urodeles. The parietals are broad and large bones, like

the frontals with nearly parallel sides, overhanging, for the most part, the open temporal region.   There is no parietal foramen. They are gently convex from side to side.   From this posterior suture the upper surface of the skull turns downward at an angle of about twenty degrees, so as to bring it nearly parallel with the plane of the lower margins of the mandibles.   Three rather large bones are seen here, a median unpaired one and two larger lateral ones.   The median bone is broader in front than behind and borders the large foramen magnum ; it doubtless corresponds to the median cartilage found in many urodeles, called the supra-occipital usually, by Gaupp the tectum synoticum.   The lateral

FIG. I.   *Lysorophus tricarinatus*, skull from above, enlarged three diameters.

bones are larger, of an irregularly square shape with a hook-like prolongation exteriorly behind, turned downward back of the squamosal.   They must be identified as "epiotics," a bone rarely if ever found separate in the modern batrachians.   The squamosal (paraquadrate of Gaupp) unites, by a nearly straight antero-posterior suture, with the parietal and epiotic and then turns downward, forward and a little outward, narrowed and more rod-like below.   There is some doubt of its union with the quadrate, but the division seems apparent on each side.   With this interpretation, the quadrates are small bones, about twice as

long as wide terminating in the cotylus, and perforated a little
above the lower extremity by a foramen. The double occipital
condyles are sessile, each with an oblique, flattened articular face
looking inward and backward. Just in front of the condyles ex-
teriorly there is a small foramen for the vagus, in front of which
there is a large vacuity for the ear opening, partially or imper-
fectly closed in front by this combined bone. Above, the bone
sends a triangular prolongation inward to the lower edge of the
supraoccipital, bordering the hind margin of the epiotic. The
large foramen magnum is thus bordered as in modern urodeles,
nearly completely, by the exoccipital. Rather closely applied
to this margin is a pair of triangular bones meeting roof-like in
the middle above and terminating below in an angle a little above
the condyles. They occupy the position of, and doubtless are the
so-called proatlas bones, displaced to form the " gular plates "
of Broili. The basioccipital bone I at first thought to be ossified,
but further examination convinces me that the broken surface
seen in the specimen between the condyles below is the broken
off anterior end of the atlas. A like condition was found by
Broili in his specimens, but he interpreted the structure as that
of a broken off occipital condyle. Furthermore, a little in front
of this fractured surface is seen the hind margin of a thin trans-
verse plate, the parasphenoids.

In the palatal region are lying four pairs of branchial bones,
with no indications whatever of so-called gular plates. The posi-
tion and relations of these bones are well shown in the accompany
ing photograph (Fig. 3). The outer pair lying close to the inner
margins of the mandibles, have the posterior end thickened and
recurved, hook-like, to abut against or approach the hind side of
the quadrate. I would take them to be ceratobranchials save for
the fact that a pair of nearly square bones very clearly articulate
with the anterior ends, which must be ceratobranchials. To the
inner side, and progressively more posterior, lying symmetrically,
are three pairs of epibranchials the inner and hindmost represented
in the specimen only by their anterior ends, the posterior por-
tions broken off with the altas. The two outer pairs, at least,
are thickened and truncate at each end, and are partly hollowed
or cancellated, like all other bones of the skeleton. The first of

these pairs also seems to have a thickened and recurved posterior
extremity.   The mandibles are rather stout, extending a short
distance back of the cotylus, expanded and flattened, somewhat
spout-like in front.   Each bears about twelve, conical, simple teeth
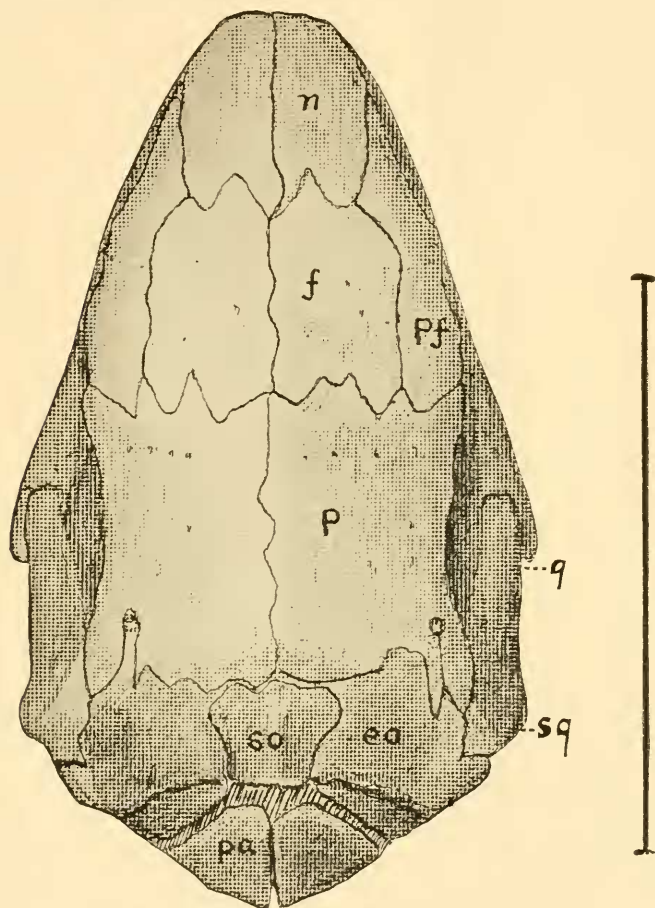on the anterior, somewhat concave margin, which is about two

Fig. 2.   *Lysorophus tricarinatus*, skull from above, enlarged five diameters.   *n*,
nasal; *f*, frontal; *pf*, prefrontal; *p*, parietal; *so*, supraoccipital; *eo*, epiotic; *pa*,
proatlas.

fifths the length of the mandible ; the teeth are directed some-
what obliquely outward.

The sides of the skull are in a nearly vertical plane, directed

somewhat obliquely outward posteriorly. The squamosal and quadrate, extending downward, forward and a little outward, meet the cotylus of the mandible a little back of the middle of the skull. Opposite the mandibular teeth in front are the narrow maxillæ, with teeth like those of the mandibles. They end freely and acuminately behind, and if connected at all with the bones of the upper part of the skull, the connection was small and slender and situated far forward. The whole side of the skull, from in front of the squamosal and quadrate seems to have been unossified; there are no jugals nor quadratojugals, and no temporal arches. The premaxillæ are also very slender, with four or five small teeth on each side. The position of the eyes was far forward, in the narrow space between the maxillæ and the prefrontals, and it is quite certain that these organs must have been very small. The nares also must have been minute and situated far forward, probably between the nasals and the premaxillæ near the middle line. Altogether, in life, save for its greater narrowness and more snake-like appearance the whole head must have been strikingly like that of *Necturus*.

Vertebræ. — The centrum is moderately elongated, deeply biconcave with persistent notochord, wholly without trace of hypocentra. In the middle below there is a median rounded keel, concave longitudinally, with a deep pit or fossa on each side reaching nearly to the internal cavity. On either side there is another, more slender carina, bounding the fossa above, with a more shallow concavity above it. The pedicel is elongate anteroposteriorly, the neural canal large. The centrum has no parapophysial facet or process for the rib. A little below and back of the anterior zygapophyses is the diapophysis, a flattened process directed anteriorly and a little downward, with the extremity thickened and a little rounded; they are short. The arches are depressed, a little convex in the middle anteroposteriorly, but without spine, the two sides separated by a persistent median suture, and the two bones are usually drawn somewhat apart, like the bones of the skull. The zygapophyses are rather large, flattened on their articular surface and are directed somewhat inwards or outwards. The ribs are large, flattened proximally, more cylindrical distally and are hollow. They have an

anterior angulation or curvature near the proximal third, this third being directed more obliquely backward. There are no traces of abdominal ribs in the numerous specimens examined, nor any of dermal plates, save in the case already spoken of, plates evidently belonging with a small mandible near them of an apparently different type from that of *Lysorophus*.

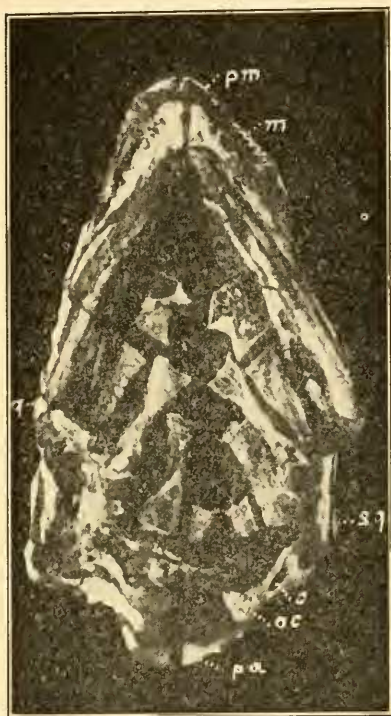The terminal part of the tail, which is preserved in one speci-

FIG. 3. *Lysorophus tricarinatus*, skull from below, enlarged five diameters. *pm*, premaxilla ; *m*, maxilla ; *sq*, squamosal ; *o*, otic fenestra ; *oc*, occipital condyle ; *pa*, proatlas.

men, ends rather gradually, tapering to a point. In the seventeen vertebræ of the series there are no ribs and no diapophyses, or very rudimentary ones anteriorly ; and I can find no traces of chevrons. Characteristic figures of the vertebræ and ribs will be found in the cited papers of Case.

That *Lysorophus* is not a reptile requires no argument — the

unpaired supraoccipital, the absence of pineal foramen, quadra-
tojugals, jugals, postfrontals, temporal arches, the evidently large
parasphenoid, the double occipital condyles, paired branchials,
neurocentral, single-headed ribs, etc., are positive evidence that
the animal is not only not a reptile but that it is related to the
modern urodele amphibians. In skull structure the characters are
urodelan in every detail save the separated "epiotics," the inter-
calary of Cuvier, Vrolik and Cope, the paroccipital plates of
Baur, the posttemporals of Broom ; and this separation is pre-
cisely what would be expected in the early urodele. The ex-
occipitals otherwise seem to be a single bone in *Lysorophus*, but
it is very probable that they are the result of an early fusion of
the exoccipitals, paroccipitals and proötics. The squamosals and
quadrates have the position and relations of modern salamanders,
the quadrate rather better ossified than is usually the case. That
the supraoccipital should be ossified is, also, what might be ex-
pected. The remarkable fact that this bone should be unpaired
while all the remainder of the bones of the skull are very loosely
joined, as also the fact that the corresponding element in the
urodeles is cartilaginous would seem to preclude its identification
with the paired supraoccipital plates, the postparietals of Broom,
of the Stegocephalia, rather favoring Gaup's contention of the
nature of his *tectum synoticum*.

The tricarinate structure of the vertebral centra is quite aber-
rant for a reptile, but not remarkable for a urodele ; so also is
the sutural division of the neurocentra, and, for the Permian, the
neurocentral attachment of the single-headed ribs. The only
aberrant character to distinguish *Lysorophus* from the Urodela is
the long and rather broad ribs, unknown among these modern
animals or their possible ancestors the Branchiosauria. It is,
however, very evident that the earliest ancestors of both these
groups must have long ribs, and their persistence in *Lysorophus*
would be nothing remarkable. Nor do I think it impossible that
Lysorophus and its immediate kin may have developed long ribs
from the earlier short ones. Certain it is that this character
alone, and it is the only aberrant one, should not exclude
Lysorophus from the Urodela, though it may necessitate a slight
revision in the definition of the group. That *Lysorophus* cannot

be classed with any of the divisions of the so-called Stegocephalia is quite as evident as its exclusion from the Reptilia ; and upon the ribs alone the formation of a new order of Amphibia would not be at all justified.

That the genus represents a distinct family of the Urodela is of course obvious.   Broili, under the erroneous supposition that it is a reptile of the order Rhynchocephalia gave to it the name Paterosauridæ, to indicate its " paternal " relationship with the reptiles.   But this name was chosen in direct contravention of the rules of zoölogical nomenclature, since it is not represented by a genus in the group, and since any one is at entire liberty to apply the stem as a generic name in another group.   The name is not tenable, and should be replaced by Lysorophidæ.

The condition in which the remains of so many of these animals are found, numerous series intermingled in vertical and lateral curves, is I think conclusive evidence that death overtook the creatures in the drying up of ponds and pools of water. That the animals were snake-like in life is of course proven by the long connected series of vertebræ of nearly uniform size. That they had but feeble power of sight is also assured by the very small size of the eyes.   That they were perenni-branchiate is I believe also extremely probable from the large size of the branchiæ, and the manner in which these creatures represented by their known remains met their death.   Doubtless also they were bare skinned and more or less mud burrowing in habit.   That *Lysophorus* stood in direct ancestral relationship to such forms as *Necturus* or *Proteus* is rather improbable, but that it was very close of kin to the ancestors of these forms I do believe to be very probable.

Salamander-Like Footprints from the Texas Red Beds.
(Fig. 4.)

Recently, Miss Augusta Hasslock, of the Abilene, Texas, High School, has had the kindness to send me a number of thin red shales showing abundant markings of raindrops, worm or other tracks and footprints which must have been made by some sala-mander-like creatures of small size.   The horizon is assumed to be Permian, but the fact that the shales occur not far below the

Cretaceous, inclines me to the belief that it will eventually be found to be Triassic.   Enlarged photographs are given of some of the best of these numerous prints.   The reverse of those at *a* and *b* are shown in *a*[1] and *b*[1].   In the lower, left corner is shown the figure of a much larger print.   It will be observed that the prints occur in pairs, one with clear evidence of five, the other with but four toes, from which the conclusion is justified that the crea-

FIG. 4.   Footprints from the red beds of Texas, near Abilene, enlarged about one third.

tures were tetradactyl in front, pentadactyl behind, as were the Branchiosauria and as are the Urodela of to-day.   Whether or not they were real salamanders which made the prints, or branchiosaurs, cannot be determined, but I am inclined to believe, in the light of the evidence presented by *Lysorophus*, that the origin of

some or all of these prints is due to real salamanders of modern type.

Ventral Ribs in Labidosaurus Incisivus. (Fig. 5.)

In a recent paper [1] I stated my belief that ventral ribs would eventually be found in some of the forms now classed in the rather heterogenous group known as the Cotylosauria, and I suspected that the specimen of *Labidosaurus* therein described presented such evidence, but could not be sure. This evidence has, however, been made clear by further preparation of that specimen. In the removal of the matrix from the under side of the pubes a small fenestra of accidental origin was found, and in this

Fig. 5.   Ventral ribs of *Labidosaurus incisivus*, enlarged about two diameters.

space, that is originally between the front end of the plate-like pubes and the vertebræ, are seen abundant evidences of small slender ribs, of some of which I give herewith a photographic illustration.   At this spot seven ribs are seen lying closely together and parallel, directed from the anterior outer corner of the pubis inward and backward.   Still further forward, and the continuation of these series, are further evidences of the same sort. The ribs are much smaller than I had expected to find them, but it is clear to me that the whole under side of the abdomen was enclosed in a closely set armor of slender ossified ribs.   This char-

[1] *Journal of Geology*, XVI., p. 148, 1908.

acter adds another evidence of the relationship between the Procolophonia and *Labidosaurus*, and destroys its value as a group distinction.

Addenda. — Texas Permian Fields, September 25. Since the manuscript of the foregoing left my hands I have seen the recent paper by Case (Bull. Amer. Mus. Nat. Hist., xxiv, 531, June 30, 1908), in which he recognizes the amphibian nature of *Lysorophus*, figuring the skull with its exposed palate. He does not, however, discuss the relationship of the form and we differ in the interpretation of some of the bones.

Within the past week Mr. Miller, my assistant, has discovered two deposits of the species herein described from which cartloads of the peculiar nodules might be had for the digging. In two other places I have found them less abundantly. In examining the selected material, I have detected a small limb, very *Necturus*-like with four metapodials and epipodials in place, the mesopodials evidently unossified. It is of course possible, but not probable, that the limb is an accidental intrusion of some other small amphibian. My conviction is that the Lysorophidæ should be included in the Ichthyoidea.

FURTHER STUDIES ON THE ELIMINATION OF THE GREEN BODIES FROM THE ENDODERM CELLS OF HYDRA VIRIDIS.

D. D. WHITNEY.

In a recent paper I called attention to the fact that when green hydras are kept in a 0.5 per cent. solution of glycerine for several days they gradually lose their green color and become colorless.[1] The green bodies were observed to be thrown out of the enteric cavity through the mouth but it was not determined how they became separated from the endoderm cells in which they are contained. It was a matter of conjecture whether the endoderm cells became detached from the walls of the enteric cavity and carried the enclosed green bodies with them, subsequently disintegrating and liberating the green bodies in the enteric cavity, or whether the endoderm cells became ruptured and let their contents flow into the enteric cavity and then out through the mouth.

A microscopical study of the endoderm cells of both the normal green hydras and the green hydras that had been in a 0.5 per cent. solution of glycerine from one hour to about three weeks gave the following results :

In the normal hydras the endoderm cells are about as long as broad and each contains a large vacuole at its inner end. Nearly all of the green bodies are at the base of the cells. Figs. 1 and 2 show respectively in a cross and a longitudinal section the condition of the endoderm cells in green hydras that were starved for fourteen days in clear water. Several which were starved only thirty-six hours were sectioned but the endoderm cells did not differ noticeably from those in the green hydras that were starved for two weeks. The animals were allowed to remain without food in order that the endoderm cells, free from food, might be compared with those of animals that had been in the glycerine solutions for the same length of time without food.

[1] BIOLOGICAL BULLETIN, 1907, XIV.

When green hydras are put into the glycerine solution the endoderm cells become larger. As the cells are closely packed together their expansion laterally is prevented. Consequently becoming larger they push out into the enteric cavity, becoming several times as long as in the normal animals. Fig. 3 shows the condition of the endoderm cells of a green hydra that had been in the glycerine solution for one hour. Some of the cells are about twice the length of those in normal hydras but otherwise they seem to be similar.

In Fig. 4 the endoderm cells are much longer and more narrow than in the preceding case. This hydra had been in glycerine solution for three hours. In Fig. 5 the endoderm cells are about the same size as in Fig. 4 but the interior of the cells is filled with a very fine granular substance and the green bodies are scattered about in this substance especially in the distal two thirds of the cells. Very few green bodies were seen near the free end of the cells. This section was from a hydra that had been in the glycerine solution for sixty hours.

The condition of the endoderm cells of hydras that were rendered entirely colorless by being kept in the glycerine solution for eighteen days or more, Fig. 6, differs only from the endoderm cells of hydras that had been in the glycerine solution for sixty hours in having no green bodies in the cells.

Each endoderm cell doubles its size at least within an hour after being put into the glycerine solution as is seen in Fig. 3. As it remains longer in the solution it becomes extended until it is ruptured and owing to the pressure of the adjacent cells extrudes much of its contents into the enteric cavity. As soon as there is an equilibrium of pressure the rupture quickly heals or regenerates thus making the cell intact again. Soon after it is whole it swells again until it is ruptured a second time and discharges more of its contents, including the green bodies, into the enteric cavity. This process is repeated as long as the animal is kept in the glycerine solution and if kept too long until its death. By this repeated process of the rupturing of each endoderm cell and the discharge of its contents all the green bodies of each cell are finally eliminated and the cells remain colorless.

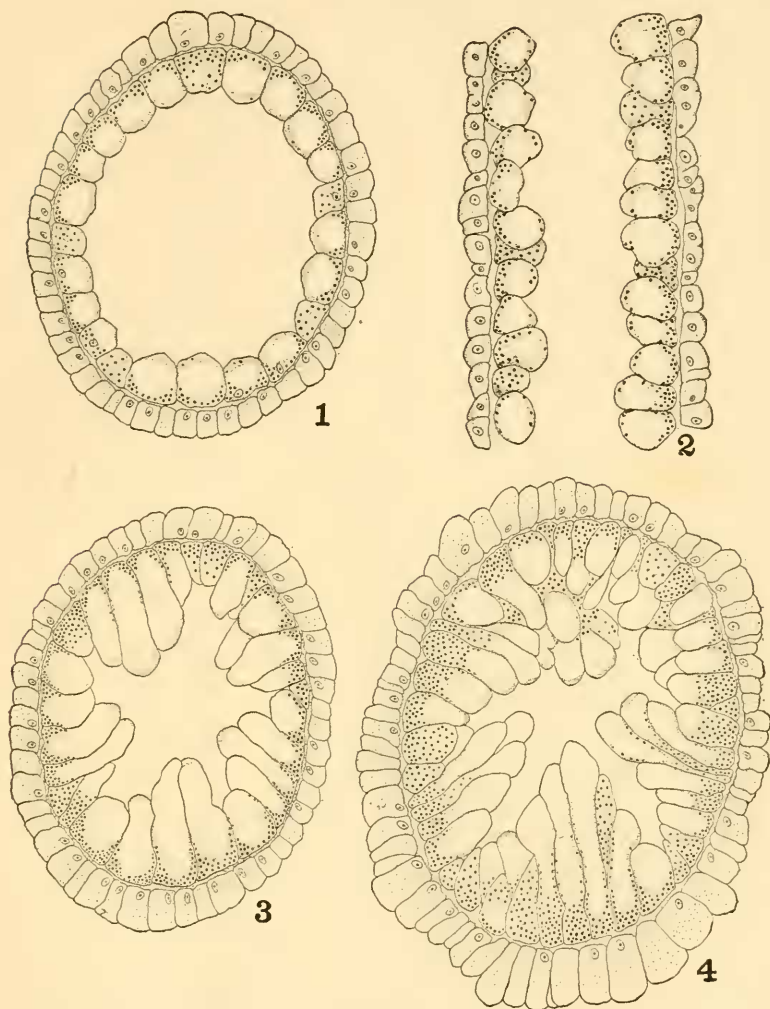The green bodies have been seen being ejected through the

FIG. 1. Cross section of a green hydra that had been without food for 13 days.

FIG. 2. Longitudinal section of a green hydra that had been without food for 13 days.

FIG. 3. Cross section of a green hydra that had been without food for 36 hours and then put into a 0.5 per cent. glycerine solution for 1 hour.

FIG. 4. Cross section of a green hydra that had been without food for 36 hours and then put into a 0.5 per cent. glycerine solution for 3 hours.

mouth of living hydras which were in glycerine solution. They were also found in greater or less numbers in the enteric cavity

of the hydras that were sectioned and studied. They always seem to be free in the enteric cavity but sometimes they are mixed with a substance which resembles the granular contents of the endoderm cells. No free endoderm cells were ever seen in the enteric cavity.

Professor W. J. Gies was kind enough to perform some experiments for me in which blood corpuscles were put into a 0.5 per cent. solution of glycerine made with physiological salt solution. Upon measuring the diameters of the corpuscles both before and after putting them into the glycerine solution it was determined that if there was any change it was a slight shrinkage but never any enlargement of the corpuscles.

When these results of the effect of glycerine on blood corpuscles are compared with those obtained on the endoderm cells of hydras which were also kept in the same percentage of glycerine solution it is seen that the results are opposite — the corpuscles shrink and the endoderm cells become larger.

The shrinking of the corpuscles is probably due to an increase of the osmotic pressure of the solution caused by the addition of the glycerine and is purely a physical change.

The enlargement of the endoderm cells of hydras might be explained as due to the glycerine acting as a stimulus to the cell and causing certain vital processes in it to become active which result in a large and rapid absorption of water by each cell. The cells react to this stimulus as long as the animals are kept in the glycerine solution. Thus this change could be called a physiological one brought about by the stimulation of living processes in the cells.

Some cells were seen which had little protuberances or outpocketings on their inner free ends which looked as though they might be weak places in the cell wall that were forced out by the increasing pressure from within. Doubtless the ruptures occur at these places.

As it is a well-known fact that hydras have extraordinary powers of regeneration in the closing of wounds, as when their bodies are cut into two or more parts, and also in the replacing of lost parts, the assumption that the ruptured places in the endoderm cells close and grow together quickly is not, I think, an improbable assumption.
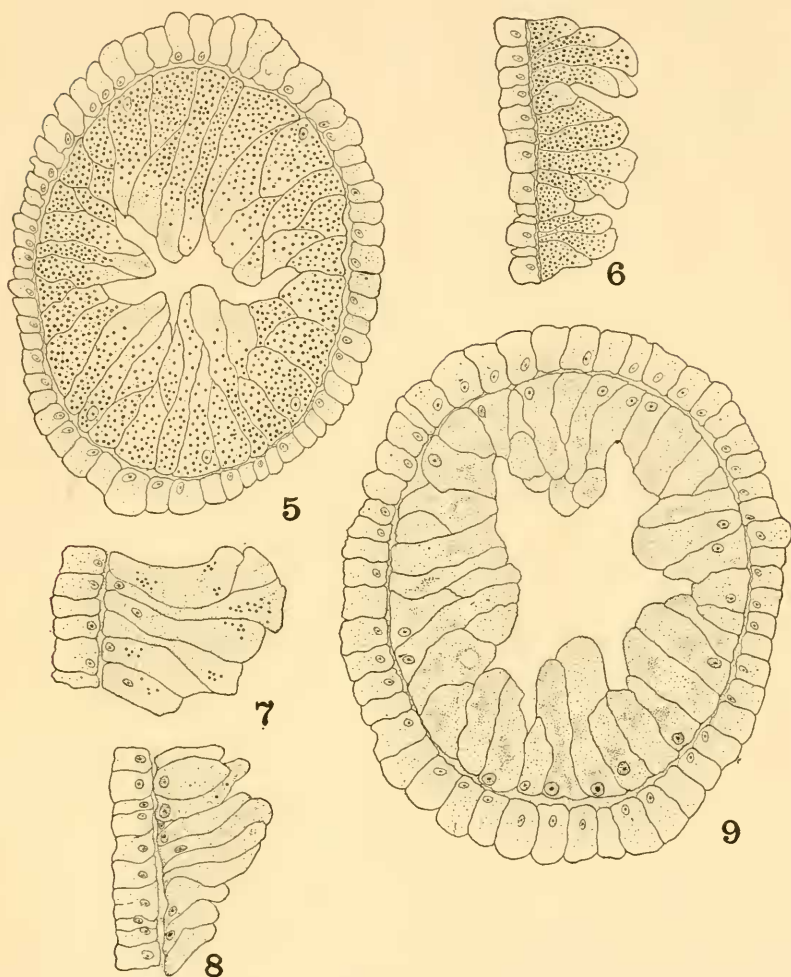
FIG. 5. Cross section of a green hydra that had been in a 0.5 per cent. glycerine solution for 60 hours.

FIG. 6. Portion of a longitudinal section of a green hydra that had been in the glycerine solution for 60 hours.

FIG. 7. Portion of a longitudinal section of a hydra that remained slightly green after being in a 0.5 per cent. glycerine solution for 13 days. Several groups of green bodies are seen in the endoderm cells.

FIG. 8. Portion of a longitudinal section of a hydra that was green when put into a 0.5 per cent. glycerine solution in which it remained 13 days and was rendered colorless. Only two green bodies seen in this section.

FIG. 9. Cross section of a hydra that was green when put into a 0.5 per cent. glycerine solution in which it remained 18 days and was rendered colorless. No green bodies are seen in this section.

Whatever the exact process may be it is certain that the endoderm cells remain in a greatly distended condition and lose all of their green bodies, many of which are found free in the enteric cavity.

ZOÖLOGICAL LABORATORY,
COLUMBIA UNIVERSITY,
NEW YORK CITY, May 29, 1908.

BIOLOGICAL BULLETIN

THE HOMING OF THE BURROWING–BEES (ANTHOPHORIDÆ).

C. H. TURNER.

INTRODUCTION.

The researches about to be described were conducted for the purpose of determining how the burrowing bees compare with the ants and the mud-dauber wasps in their method of finding the way home. During most of the month of August, 1908, from five to ten hours a day were devoted to this study. This made it possible to conduct several series of experiments. Since all of the series led to similar conclusions, only two of them will be recorded. The majority of the experiments were conducted upon a species of *Melissodes* Latrl., many nests of which existed in an abandoned garden of the Haines Normal School.

SERIES A. EXPERIMENTS ON MELISSODES.

These experiments were conducted in a deserted garden. Before beginning the experiments proper, numerous preliminary observations were made for the purpose of obtaining information that would be helpful in conducting and interpreting the experiments.

Bearing in mind Bohn's assertion that the flights of certain Lepidoptera are anemotropisms and phototropisms,[1] much attention was given to the flight of these bees.

When these anthophorids are busy at work, the flight is certainly neither an anemotropism nor a phototropism, for neither the movements nor the orientation of the body bear any constant relation to either the direction of the wind or to the rays of the sun.

[1] M. Bohn, "Observations sur les Papillons du Rivage de la Mer," *Bull. de L'Institut Général Psychologique,* 1907, pp. 285–300.

Observation soon informed me that each burrow was visited by bees at approximately regular intervals. Some of the nest-holes were visited by a bee about once in twenty minutes, other nests were visited more frequently. I soon discovered that where each interval between the visits was much less than twenty minutes, two or more bees occupied the burrow in common ;[1] but that where the interval was twenty minutes or more, then only one bee was occupying the burrow. This enabled me to select, with a certainty, burrows that were occupied by only one bee.

The following series of experiments was performed upon a bee that occupied a burrow all to itself. The burrow was situated in a small barren spot and surrounded by a few blades of grass, which partially covered the opening. The heads of several stalks of grass overlapped the barren spot. The bee arrived at 9:35 A. M. and immediately entered the burrow. At 9:37 A. M., it departed again for the field, without stopping to explore the surroundings of the nest-opening.

Experiment 1.

While the bee was afield, a rectangular piece of white paper, 12 cm. by 8 cm., in the center of which was a hole 13 mm. in diameter, was so adjusted over the nest as to have the hole in the paper coincide with the opening of the burrow.

At 9:55 A. M., the bee arrived with its burden of pollen. Instead of entering the nest, it circled around and around. It then hovered, momentarily, over the white rectangle and then described yet wider circles in the air. This behavior was repeated several times. At 9:57 A. M., two minutes after its return from the field, the bee entered the nest. On again departing for the field, at 10:00 A. M., the bee hovered a while above the paper that surrounded the nest ; then, after making several turns of a helicoid curve, flew away.

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[1] To determine how many bees were occupying a burrow, I would plug the opening and then observe it carefully for an hour or longer. The bees, on returning, would circle about the nest. After a while they would usually try to dig around the plug. By counting the bees that appeared and tarried it was easy to determine how many bees were occupying the burrow. When the required information had been obtained, the plug was removed.

Experiment 2.

The same conditions as in experiment one.

At 10:20 A. M., the bee arrived from its trip, hovered for less than half a minute and then dropped into the nest. At 10:24 A. M., the bee departed, without stopping to explore the surroundings of the nest.

Experiment 3.

About four inches to the east of the nest opening, a hole was made in the ground. Over this hole was placed the piece of white paper, with the hole in the center, which was adjusted over the nest in experiment two. A piece of water-melon rind, with a thirteen mm. hole in the center, was so adjusted over the nest as to have the hole in the rind coincide with the opening of the burrow. One half of the rind was brown, the other half yellowish green; the line dividing these two colors bisected the hole in the center of the rind.

At 10:47 A. M., the bee arrived with its burden of pollen. It hovered above the melon-rind for a moment, then circled about the place. At 10:48 A. M., after a search of one minute, the bee entered the nest. On leaving the nest at 10:59 A. M., the bee examined carefully the surroundings before departing.

Experiment 4.

While the bee was afield, the piece of water-melon rind was removed and a rectangular piece of white paper, eight cm. long and five cm. wide, was arched over the nest in such a way as to form a tent six cm. high, the east and west ends of which were open. The rectangular piece of white paper, with the hole in the center, which was left in the same position as in experiment three, was situated just in front of the eastern opening of the tent.

When the bee arrived, at 11:15 A. M., it circled about for two minutes [until 11:17 A. M.] and then dropped into the hole over which the rectangular piece of paper, with the hole in its center, had been adjusted. It emerged at once and, after circling about for a short time, reëntered the same hole. It emerged immediately. Finally, at 11:18 A. M., three minutes after arriving on the spot, the bee entered the tent, through the eastern opening, and dropped into the burrow. On emerging from the nest, at 11:31 A. M., the bee hovered a moment inside of the

tent.   It then passed out of the east opening and hovered for a
few seconds above the tent.   Then, keeping close to the top of
the grass, it flew about for a while in a sub-helicoidal curve and
then flew away to the field.

EXPERIMENT 5.

The same conditions as in experiment four.

At high noon, the bee arrived at the southern end of the tent.
After hovering but a moment, it flew around to the front and
entered the tent through the eastern opening.   It then right-about
faced and dropped into the burrow.   On leaving, at 12:08 P. M.,
it hovered a moment inside of the tent, then departed without
further exploration.

EXPERIMENT 6.

The same conditions as in experiments four and five.

On arriving from the field, at 12:28 P. M., the bee flew im-
mediately, over the top of the tent, to the eastern opening and then
directly to the burrow.   It did not turn about before entering the
nest.   At 12:34 P. M., it departed without exploring the sur-
roundings ; it did not even hover in the inside of the tent.

EXPERIMENT 7.

The same conditions as in experiments four, five and six.

At 12:52 P. M., the bee appeared at the eastern entrance to
the tent.   Immediately the bee entered the tent and alighted on
the ground.   At once it flew upward and dropped into the bur-
row.   At 12:59 P. M., it departed, without exploring the sur-
roundings.

EXPERIMENT 8.

*The rectangular piece of white paper, with a hole in its center,
was left in the same position as in experiments five to seven inclusive ;
but the tent, over the nest opening, was so adjusted as to have its
open ends face north and south.*

At 1:25 P. M., the bee arrived at the eastern end of the tent.
It immediately flew around to the southern entrance of the tent
and entered the burrow.

The above eight experiments were performed August 14, 1908.
On the next day (August 15) the following five experiments were
performed with the same individual.

Experiment 9.

The same conditions as in experiment eight.   The apparatus had been left in position for twenty hours.   Something had trampled the tent to the ground.   It was readjusted to the proper height.

At 9:34 A. M., August 15, the bee arrived, hovered but a moment, and then entered the tent, through the southern opening, and dropped immediately into the burrow.

Experiment 10.

While the bee was afield, several stalks of grass were removed from the west side of the tent; thus increasing the width of the barren patch that surrounded the burrow.   The other conditions were the same as in experiment nine.

At 9:54 A. M., the bee arrived from the field.   It circled about fully a minute before entering the tent.   It then passed through the northern opening and immediately dropped into the burrow. On departing, at 9:59 A. M., the bee did not stop to explore the surroundings.

Experiment 11.

The same conditions as in experiment ten.

On arriving, at 10:18 A. M., the bee circled about for a moment and then, entering the tent through the southern opening, immediately dropped into the burrow.   At 10:23 A. M., the bee departed, through the southern opening, without stopping to explore the surroundings.

Experiment 12.

While the bee was afield, the tent, with the open ends facing north and south, was placed two inches to the west of the nest-opening.   A rectangular piece of black paper, 12 cm. long by 8 cm. wide, with a hole 13 mm. in diameter in its center, was so adjusted over the nest as to have the hole in its center coincide with the opening of the burrow.   The rectangular piece of white paper, with the hole in its center, was left in the same position as in experiment eleven.

At 11:16 A. M., the bee arrived from the field, hovered a few seconds above the black paper, then dropped into the nest.   On leaving, at 10:51 A. M., it hovered a short while before departing.

Experiment 13.

While the bee was afield, the rectangular piece of white paper was so adjusted over the nest as to have the hole in its center coincide with the opening of the burrow. The rectangular piece of black paper was placed in the position occupied by the white rectangle in experiment twelve. The tent was left in the same situation as in experiment twelve.

On arriving, at 11:16 A. M., the bee hovered above the white paper, over half a minute, before dropping into the burrow. On departing, at 11:23 A. M., it hovered quite a while, examining the surroundings.

Experiment 14.

While the bee was afield, all accessories were removed from the neighborhood of the nest and the barren patch covered with a thin layer of freshly mown grass. Care was taken to leave the opening to the burrow uncovered.

The bee arrived from the field at 11:50 A. M. and began to fly about in a sub-helicoidal curve. The radii of this curve became, irregularly, longer and longer until the bee had reached a fence fifteen feet away. Then the bee approached the nest and flew about in curves, the radii of which became, irregularly, shorter and shorter. At 11:52 A. M., after a search of two minutes, the bee dropped into the nest.

Series B.

The bee upon which this series of experiments was conducted was a much smaller insect than the *Melissodes* sp.? upon which the above experiments were performed. One of those tragedies, which are so common in the insect world, brought this bee's labors to a close before I was ready to capture it; hence it was impossible to determine the genus to which it belongs. I am not even sure whether it is a member of the Anthophoridæ or of the Andrenidæ. In this connection, however, the exact name is a matter of little weight; for, although there are generic, specific and individual peculiarities of behavior, yet the general habits of all the burrowing bees are so similar, that it would be illogical to suppose that the method of finding the way home was not essentially the same in all genera.

Several of the walks of Haines Normal School, Augusta, Ga., are separated from the adjacent flower beds by bricks inclined in such a manner as to form a serrated border of wedges of bricks ; each wedge being about two inches high and something over four inches wide at the base.   One of these flower beds, which was quite sandy, contained, in its center, a patch of nasturtiums. About two feet from the bricks, and parallel to the border, there extended, throughout the bed, a narrow row of violets.   The remainder of the bed was bare.   In a barren spot in this bed, adjacent to an inverted tin cap of a coca-cola bottle, and within an inch of the northern face of one of the bricks that formed the serrated border, a burrowing-bee had excavated a burrow.   The nest was discovered at nine A. M., August 8, 1908.   The sun was shining brightly at the time ; but the nest, which was situated a little to the west of the southern wall of a large three-story brick building, was in the shadow.   A gentle breeze was blowing from the south.   At the time mentioned, the bee was busy collecting pollen and storing it in the burrow.   The flowers from which it obtained its supply must have been quite remote, for it required about thirty minutes to make a trip.

For convenience, the brick before which the burrow was located was designated zero and bricks to the west of it W_1, W_2, W_3, etc., in regular succession.   Likewise the bricks to the east were named E_1, E_2, E_3, etc.

The field from which the bee obtained its pollen was situated to the south of the school, and the burrow of the bee was located to the north of the brick border.   On arriving from its forage, the bee would reach the brick border at, or near, brick W_{10}.   It then would turn about so as to face the northern surface of the brick border.   Then hovering at about an inch and a half from the ground and about the same distance from the bricks, the bee would sidle along.   Usually its movement was toward the east ; but, occasionally, it would retrograde westward a short distance and then resume its eastward progress.   On reaching the brick before which its nest was located, it would drop immediately into its burrow.   After remaining in the burrow a few minutes, the bee would depart, without stopping to explore the surroundings.   Several trips of the bee were observed carefully and in

each case the behavior was essentially the same. In its flight, neither the orientation of its body nor the direction of its movements bore any constant relation either to the direction of the wind or to the rays of the sun.

EXPERIMENT I.

While the bee was afield, with a stick of the same diameter as the burrow, I punched, in the ground in front of bricks W_1 and E_1, holes which bore the same relation to each of those bricks that the burrow opening did to brick zero. The inverted tin cap of a coca-cola bottle was removed from its place beside the burrow and placed, in the same relative position, at the side of the hole which I had made in front of brick W_1.

The bee, on returning from the field, arrived at brick W_{10}. It then turned around so as to face the northern surface of the brick border. Then hovering at about an inch and a half above the ground and at about the same distance from the border, it sidled along. Most of the time it moved towards the east; but, occasionally, it retrograded westward, for a short distance, and then resumed its eastward progress. On reaching brick W_1, it dropped, at once, into the hole which I had made. It emerged at once and continued its eastward course until it reached its burrow, which it entered. It tarried in the nest a few minutes, then departed, without stopping to explore the surroundings, for the pollen field. Evidently, a slight topographical change of the neighborhood of the nest caused the bee to enter a false burrow, which it discovered was not its own.

EXPERIMENT II.

While the bee was afield, I punched holes, similar to those described above, before bricks W_2, W_3, W_4, W_5, and bricks E_2, E_3, E_4 — one hole before each brick. For descriptive purposes, I shall call the holes before bricks W_1, W_2, W_3, etc., respectively L_1, L_2, L_3, etc., and those in front of bricks E_1, E_2, E_3, etc., R_1, R_2, R_3, etc.

On returning from the field, the bee arrived at brick W_{10}. It then turned about so as to face the northern surface of the border, and, hovering and sidling, in the manner described in experiment I., it moved eastward until it reached hole R_1, into which it

dropped. Emerging at once, it hovered a moment and then dropped into the same hole. Again emerging it moved westward and dropped into its burrow. On emerging from the nest, it went immediately afield.

Experiment III.

While the bee was afield, I placed, before each of the holes I had made, except holes R_3 and R_4, an inverted tin cap of a coca-cola bottle. The other conditions were the same as in experiment II.

On returning from the field, the bee arrived at brick W_9. It turned about so as to face the northern surface of the border, and, in the hovering and sidling manner mentioned above, moved eastward, hovering momentarily over holes L_4, L_3, L_2, L_1, until it reached the nest, which it entered immediately. There it tarried a moment, then departed, without stopping to examine the surroundings, for the pollen-fields.

Experiment IV.

While the bee was afield, I placed a small tent of white paper over the burrow. The tent, the whole north end of which was open, was three inches wide, at the base, two inches high and three inches long. The other conditions were the same as in experiment III.

On returning from the field, the bee arrived at brick W_8. It then turned about so as to face the northern surface of the border and then, in the hovering and sidling manner mentioned above, it moved along, hovering, in the order mentioned, above holes L_4, L_3, L_2, L_1. On reaching the tent, it retraced its steps, hovering over holes L_1, L_2, L_3, L_4. It then resumed its eastward journey. Although it had been sometime since the bee returned from the field, yet it had not entered any hole. At this stage, however, it dropped into hole R_1. Emerging, it hovered a moment and then reëntered the same hole. Emerging from the hole, it began to fly about in a random manner. Evidently it could not locate the burrow. It had passed over the tent several times, but had made no attempt to enter it.

I now removed the tent, thus leaving everything in the same condition as in experiment III.

In a few moments the bee reached the nest and, after hovering

a moment, entered.   On departing for the field, it spent considerable time hovering about the burrow, as though it were examining the surroundings.

EXPERIMENT V.

While the bee was afield, a rectangular piece of paper, 12 cm. long by 8 cm. wide, in the center of which was a hole 13 mm. in diameter, was so adjusted over the nest as to have the hole in the paper coincide with the burrow-opening.   The other conditions were the same as in experiment three.

On returning from the field, the bee arrived at brick W_{12} and turned about so as to face the northern surface of the border. In the hovering, halting, manner mentioned above, it sidled eastward, hovering a moment over each hole reached, but entering none.   Over the nest it hovered a little longer than it did over holes L_4, L_3, L_2, L_1 ; but, instead of entering, it continued its search eastward.   On reaching hole R_1 the bee dropped into it.   Immediately it emerged, hovered a moment, then dropped again into the same hole.   Reëmerging from hole R_1, it journeyed eastward and dropped into hole R_2.   Emerging from this hole, it passed to brick zero, hovered for about a minute above the burrow but did not enter.   It now began to roam about at random.   After the lapse of some time, it reappeared above the nest, hovered a moment and then dropped into the burrow.   On emerging from the nest, the bee hovered about for some time and then circled about the neighborhood, before departing for the field.

EXPERIMENT VI.

The same conditions as in experiment V.

On returning from the field, the bee arrived at brick W_{10}.   In the hovering, halting, manner described above, it sidled eastward, halting over each hole, but entering none.   It started to enter hole L_1, but retreated before the body was three fourths hidden. As soon as the nest was reached, the burrow was entered.

CONCLUSIONS.

It is evident that the behavior exhibited by the above experiments cannot be classed as either anemotropisms or as phototropisms, for neither the orientation of the body nor the direction

of flight bore any constant relation either to the direction of the wind or to the rays of the sun.   Many of the nests observed by me were in the sunshine a part of the day and in shadow the balance of the day, yet the bee found the nest just as readily when it was in the shadow as it did when it was in bright sunlight.

Any pronounced change made in the topography of the vicinity of the nest, while the bee is away from its burrow, is sure to cause the insect, on its return, to be forced to search about in order to find the entrance to its home [Ex. 1, 3, 4, 10, 14, I., II., IV., V.].   This is true even when the nest opening is in full view [Ex. 1, 3, I., II.].   If the proper alterations are made in the topography of the vicinity of the nest, the bee may be induced to enter, temporarily, a false burrow [Ex. 4, I., II., IV., V.]. A bee that has not been experimented upon is much more affected by slight alterations made in the topography of the vicinity of the burrow than is the same bee after a prolonged period of experimentation [cf. Ex. 1 with Ex. 13 and 14].   All of these statements militate against the old idea of a "homing instinct," against Pieron's kinesthetic reflex hypothesis and against Bethe's contention that bees are guided home by an unknown force which acts reflexly; for if either of these assumptions were true, changes made in the topography of the vicinity of the nest should not alter the behavior of the bees.

It would be erroneous to claim that these burrowing-bees find their way home by the method of "trial and error," for there is no gradual "stamping in" of an appropriate response.   When the bee, on returning home, finds the environment markedly changed, it searches until the opening of the burrow is found. Before departing again for the field, the bee makes a careful examination of the vicinity of the nest [Ex. 1, 3, 4, 13, IV., V.]. On its next return to the burrow, unless the environment has been changed in the meanwhile, the bee flies directly to the burrow in the minimal amount of time; there is none of that blundering into a solution which the method of "trial and error" demands [Ex. 2, 5, VI.].

By a process of elimination, the most consistent explanation of the above behavior is the assumption that burrowing-bees utilize memory in finding the way home, and that they examine

carefully the neighborhood of the nest, for the purpose of forming memory pictures of the topographical environment of the burrow. This assumption that the exploration of the vicinity of the nest is for the purpose of forming memory pictures is supported by the fact that such explorations are always made before beginning trips that immediately follow some pronounced change in the topography of the environment [Ex. 1, 3, 4, 13, IV., V.], and not when such changes have not been made [Ex. 2, 5, 6, 7, 10, 11]. Slight changes in the topographical environment of the burrow may, at times, effectively disturb the bee on its homeward journey, and yet not be sufficiently pronounced to cause the departing bee to pause and reëxplore the surroundings of the nest [Ex. I., II., III.].

HAINES NORMAL SCHOOL,
AUGUSTA, GA., September, 1, 1908.

OBSERVATIONS ON THE BEHAVIOR OF THE HOLOTHURIAN, THYONE BRIAREUS (LESEUR).[1]

A. S. PEARSE.

I. INTRODUCTION.

The different classes of echinoderms show in a remarkable way the extreme variations which one fundamental plan of structure may undergo in order to become adapted to different conditions of existence. Developing from a bilaterally symmetrical pelagic larva, the adult echinoderm becomes an almost perfect type of radiate symmetry, except in those forms which have a bilaterality superposed secondarily upon the typical radiate plan of structure, so that the adult becomes bilaterally symmetrical only after it has passed through the more primitive

[1] Contributions from the Zoölogical Laboratory of the University of Michigan, No. 119.

bilateral and radiate stages. Correlated with the variations in structure which are found in this group of animals, are corresponding differences in locomotion, respiration, feeding and other life processes, and the behavior of echinoderms is therefore a matter of particular interest on account of the opportunity it offers to compare the reactions of nearly related forms which have somewhat different types of symmetry. The reactions of certain stelleroids and echinoids (which are typically radiate in structure) have been carefully studied, but no observations of behavior have been made on holothurians (which are more or less bilateral) except for the brief papers of Clark ('99) and Grave (:02, :05). The writer had the opportunity, during July and August of the present year, of observing the common sea-cucumber, *Thyone briareus* (Leseur), and though lack of time prevented the observations from being very extensive and left many questions untested, it is believed that there are some points of interest in what follows. The object of the work was (1) to determine what the normal activities of this holothurian are and (2) to discover how its reactions are influenced by external stimulation. The experiments were carried on in the Marine Biological Laboratory, at Woods Hole, Mass., and my thanks are due to the director, Professor F. R. Lillie, for his kindness during the work.

II. Structural Characteristics.

In order that we may have clearly in mind the structural peculiarities of the form with which we are dealing and to gain an idea of the points in which it has departed from the typical radiate plan of symmetry, some time will be devoted to a brief review of the anatomy. *Thyone briareus* (Fig. 1) is a spindle-shaped animal which varies considerably in size, and this variation is not only dependent on the age but also on the condition of contraction or expansion. Fully extended individuals sometimes measure over twenty centimeters in length and a specimen of this size would be only six or seven centimeters long when contracted. At the posterior end there is an opening through which water is drawn into the cloaca and expelled again for purposes of respiration and excretion. The mouth is at the anterior end and is surrounded by
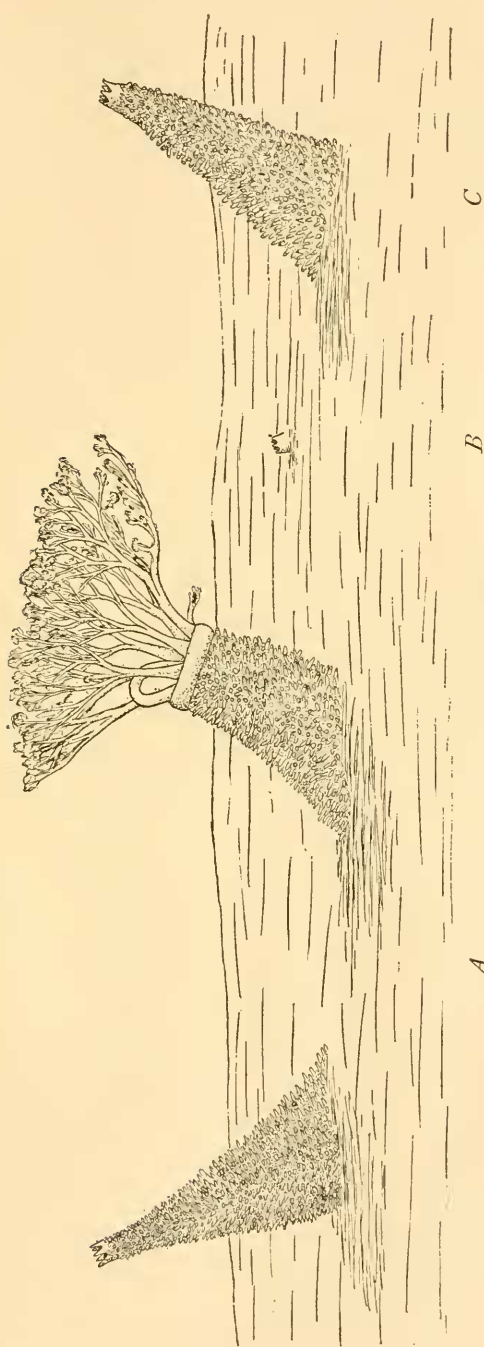
FIG. 1. *Thyone briareus.* Sketch representing three individuals buried in the mud. *A* is fully extended and both ends are visible. *B* has only the tip of the posterior end uncovered but *C* projects somewhat further above the mud.

ten dendroid tentacles which may be extended for feeding or collapsed and completely concealed by the turning in of the anterior end of the body. Just behind the tentacles is a " collar " which is without the slender tube-feet which cover the rest of the body. The tube-feet on the ventral and lateral surfaces have well developed sucking discs at their tips but such adhesive organs are not uniformly present on the dorsal side of the body. Besides this difference in the tube-feet, the dorsal and ventral surfaces may be distinguished from each other by the fact that the former is shorter than the latter and hence the ends of the body turn upward when the animal rests on its ventral side. They may be further distinguished by the difference in color (ventral being lighter), by the presence of a single median dorsal genital papilla between the bases of the tentacles, and by the fact that the two ventral tentacles are much shorter than the others. The internal organs are strikingly bilateral in their arrangement. This is shown by the right and left respiratory trees which unite and have a common opening on the dorsal side of the cloaca, by the single dorsal gonad and madreporite, and by the ventral Polian vesicles. The organs of the body wall are, on the other hand, typically radial in arrangement and hence the skeletal, muscular, water-vascular and nervous systems conform in general to the usual echinoderm type of structure. The water-vascular and nervous systems both consist of a circum-oral ring from which five radial branches extend in the body wall to the region of the cloaca. The skeletal parts consist of ten ossicles around the mouth which together form " the lantern," and of minute calcareous plates imbedded in the skin at the anterior and posterior ends of the body. The muscular system consists of five longitudinal bands, which extend from the circum-oral ossicles to the posterior end of the body, and of circular muscles which lie just beneath the skin and completely fill the space between the longitudinal muscles. The digestive tube is considerably coiled and is differentiated into four regions : an œsophagus which passes through the lantern, an expanded stomach, a slender intestine, and a musular cloacal chamber which gives rise dorsally to the respiratory trees.

From this brief synopsis of the structure of *Thyone*, it will be seen that, though we are dealing with an animal having a radiate

plan of structure, it has been modified in such a way that all of the systems of organs are more or less bilateral. There are well-differentiated anterior and posterior ends, but these are at the extremities of an axis which is horizontal instead of vertical as in most other echinoderms, for, like all holothurians, this species rests on its ventral side and the oro-anal axis is hence parallel to the surface on which it lies.

III. Methods of Response to Stimuli.

The behavior of any animal consists of the reactions which it gives in response to changes in its environment or to changes in its internal condition. It is an easy matter to change the surrounding conditions but we can interpret the internal changes which an animal undergoes as it responds to various stimuli only by its movements. Every species is limited to certain types of response by its structure, by the medium in which it lives, and by its past history. Therefore the first question to be considered is, by what reactions is *Thyone* able to respond when it is stimulated? The chief types of response will be stated briefly and the consideration of how they are brought about left for later discussion.

1. *Withdrawing Reaction.* — The reaction which is most often seen is the withdrawal of the posterior end of the body and the closing of the cloacal opening. The extent of this response depends upon various factors and it may be so slight as to be barely noticeable or it may be so marked that the body entirely disappears beneath the sand in which the animal is buried and remains out of sight for two or three minutes. Similar withdrawing reactions are performed by the anterior end of the body and also by the isolated parts, such as a single tube-foot.

2. *Extending Reaction.* — Under certain conditions the posterior end of the body becomes greatly elongated and is sometimes stretched as much as nine centimeters above the mud in which an individual lies buried.

3. *Locomotion.* — If *Thyone* is placed on a hard surface, such as the bottom of a glass dish, it attaches the tube-feet and moves across the surface and it may even climb the side of the dish. It is also able to burrow into sand or mud and may move about somewhat beneath the surface.

4. *Change in Size.* — As has been previously stated, this species undergoes marked changes in size and may shrink to a half or a third of its original volume when it is strongly stimulated.

5. *Feeding.* — Under certain conditions the circum-oral tentacles are extended and either waved in the water or swept over the surface of the mud in which the animal is buried. They are then consecutively poked into the mouth and wiped off. This reaction has been briefly described by Grave (:02).

6. *Change in Respiratory Movements.* — Water is periodically drawn through the cloacal chamber into the respiratory trees and expelled again. This series of breathing movements may be interrupted for a time or the rate may be increased or decreased.

7. *Self Mutilation.* — When the water becomes stagnant or when conditions become otherwise unfavorable the anterior end of the body is often cast off together with some of the visceral organs. The lantern, the circum-oral nerve and water vascular rings, the tentacles, and more or less of the enteric canal are frequently lost in this manner.

There are then at least seven well-defined reactions which may be used as a basis for the study of the behavior of *Thyone.* None of these responses are invariably called forth, however, when an individual is subjected to a certain stimulus. While one reaction is taking place it may exert an inhibitory influence on others, and the responses are all more or less changeable and therefore apt to vary in degree with a repetition of the same stimulus.

IV. LOCOMOTION.

1. *On a Solid Surface.* — Individuals which were moving on a solid surface were never observed to extend the tentacles and remained more or less contracted so that they were usually not more than seven or eight centimeters long. When an animal is placed on the bottom of a dish in sea water it remains contracted for a short time, but the ventral tube-feet usually become attached within a minute. The posterior end is then slowly extended and the respiratory movements begin ; the tube feet are protruded on all sides of the body and begin to wave about, and those which come in contact with a solid object attach themselves. The animal may move in any direction but the locomotion usually carries

it away from the source of the light, as *Thyone* is very sensitive to photic stimulation.   Locomotion is brought about by shortening the tube-feet after they have been extended and attached, by twisting and extending movements of the whole body, and it is also assisted by sharp waves of muscular contraction which travel from one end of the body to the other.

The tube-feet act by pulling.   They were never observed to become rigid enough to lift the body from the surface on which it rested, nor was there any pushing action, such as Jennings (:07, p. 99) described in the starfish.   There was some lack of correlation in their movements and this manifested itself in two ways.   When locomotion was taking place in a definite direction, the tube-feet were not only extended on the side towards which the animal was moving, but also over all the rest of the body. This was doubtless due partly to the fact that the tube-feet serve as organs of touch as well as of locomotion, but there were nevertheless a large number of seeking movements which were apparently of no use in locomotion.   Furthermore, some of the tube-feet which were behind as an individual moved often remained attached for some time after they could be of any help in locomotion, and, after being greatly stretched, they were actually jerked from their attachments with a snap.   They were never torn loose from the body, however, as often happens when *Arbacia* is pulled away from a solid surface.   The stimulation which brings about the attachment of the terminal discs of the tube-feet is apparently contact with a solid object.   Bits of shell, sand, and other bodies were frequently held by them for several days at a time.

In addition to the pulling action of the tube-feet, locomotion was often assisted by movements of the body.   Individuals sometimes assumed a shortened form, detached the tube-feet at one end of the body, and then elongated this free end or made slow seeking movements which were somewhat like those of a leech. This free portion of the body was then attached and the animal slowly regained its contracted form again, thus making some progress.   The sharply defined waves of contraction which commonly passed from one end of the body to the other were apparently of use chiefly in enabling the tube-feet to gain a new

attachment. A constriction might appear at either end as a ring around the body and pass to the opposite end. These rings usually moved over the body singly and a new one appeared about every three minutes on an active individual. Sometimes constrictions appeared simultaneously at both ends and neutralized each other as they met in the middle. As one of these constricted rings moved along the tube-feet were pulled from their attachments and folded into it, and when they were again extended they became fastened at points farther along in the direction of locomotion. As has been stated, *Thyone* apparently experienced some difficulty in getting the tube-feet to detach themselves at the proper time and this " ring-of-constriction " method was entirely effective in simultaneously pulling them loose in a certain region of the body. It is not intended to intimate however that the tube-feet could not be detached and moved forward without the use of these periodic constrictions.

Perhaps the most striking feature of the locomotion on a solid surface was the fact that it was without definite orientation. Individuals moved with the posterior end in advance as often as with the anterior end, and although the long axis of the body was as a rule approximately parallel with the direction of locomotion, animals often moved a long distance (as much as 12 cm.) with the body at right angles to the direction of movement, that is, they moved straight toward the right or left. The rate of locomotion was slow, the most rapid movement recorded being seven centimeters in fifteen minutes, or nearly half a centimeter per minute. In climbing up a vertical surface like the side of a dish the movements were not essentially different from those which took place when an individual was creeping on a horizontal surface.

2. *Burrowing.* — When *Thyone* is placed in a dish of sea water on a sandy bottom it usually twists and turns the body until it comes in contact with the side of the vessel. It attaches itself to the side, burrows downward, and then moves away from the side of the dish into the sand. The tube-feet are apparently of little use in locomotion on sand, and this fact supports the conclusion reached from watching their action on a solid surface, that they are effective in pulling the body along rather than in pushing

it.   Occasionally individuals were found which burrowed directly into the sand without attaching themselves to any solid object. The results of an experiment performed on July 25 are typical of the other cases of burrowing observed.   Four animals were placed in aquarium jars containing sand and sea water.   One individual burrowed straight down into the sand and covered itself in three hours ; another lay on top of the sand two hours and then took four hours to burrow ; the third individual twisted about on top for half an hour, then came in contact with the side of the jar and burrowed into the sand in two hours and a half; the fourth took four hours to reach the side and then partly covered itself in two hours.   On another occasion an animal lay on the sand eighteen hours but covered itself in two hours when placed against the side of the jar.

Burrowing is accomplished by a contraction of the body muscles and the action of the tube-feet.   When the body is fastened to some solid object, the tube-feet are attached as far down its side as possible and the body is drawn out so that it is wedge-shaped in cross-section.   The longitudinal body muscles are then contracted so that the body shortens, and the sand is forced aside as the cross-section becomes more circular in outline.   During the entire process the two ends of the body are turned upward and the animal sinks down into the sand with the dorsal surface constantly uppermost.   This method of procedure is usually repeated until the individual is completely buried, except the posterior end.   The downward movement is assisted by the passage of constricted rings from one end of the body to the other, or from both ends toward the middle, the sand thus being loosened so that the body can be " wedged " down into it.   When there is no solid object for the attachment of the tube-feet, burrowing is more difficult.   As the waves of contraction pass over the body, the sand is gradually pushed aside so that a thin portion of the ventral surface is forced downward (Fig. 2, A).   The dorsal longitudinal muscle bands and the circular muscles then contract and the ventral portion of the body expands in such a way that the sand is forced aside (B).   This same process is repeated at intervals until the animal is covered.

Thyone can move about to some extent after it is buried in the

sand. It accomplishes this in the same way that it burrows and also to some extent by bending and straightening the body. A series of experiments was carried out to ascertain how deep *Thyone* could be buried in the sand and yet burrow out. The method was to place an individual in the bottom of a jar containing sea water to a depth of 55 cm., which was the height of the jar. It was then covered with sand to the desired depth. Individuals
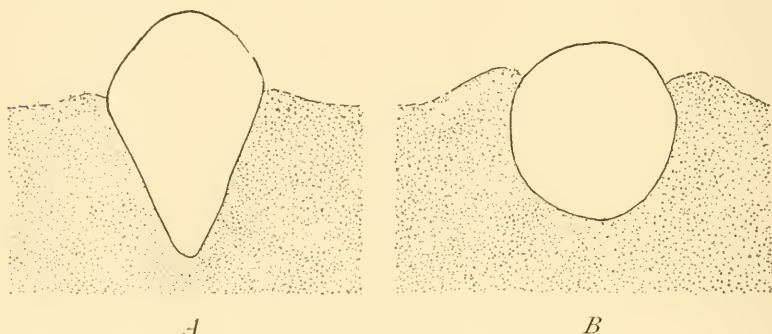

FIG. 2. Diagrams representing the shape of cross-sections in the middle of the body of *Thyone* as it burrows into the sand. The form shown in *A* precedes that shown in *B*.

were able to come to the top of the sand when covered under fifteen centimeters but none came up through twenty centimeters although ten large individuals were tested.

Clark ('99) found that *Synapta* burrowed with the tentacles and that it always went into the sand "head first." *Thyone* differs from it quite strikingly in the latter respect but this difference is perhaps no more than would be expected from the structural unlikeness between the two forms.

V. FEEDING.

After an individual has been undisturbed for some time it often extends the anterior end of the body and the tentacles and makes feeding movements (Fig. 1, *A*). In this extension the longitudinal muscles pull the lantern forward and the circular body muscles contract. The anterior end of the body is thus everted, like the turning inside out of the finger of a glove. The branched tentacles are then pushed out by the pressure of the fluids within them and the action of the muscles in their walls.

The two short ventral tentacles are most active and constantly move in and out of the mouth opening, while the larger tentacles wave about more slowly. The latter are moved through the water or scraped over the bottom and then consecutively wiped off in the mouth. When one of these large tentacles is wiped off, its proximal end is pushed into the mouth first and the distal branches follow. Before one tentacle has emerged, another is usually being pressed down upon it ready to enter. Sometimes two of the large tentacles bend toward the mouth at once but in no case were two seen to enter the mouth simultaneously, one of them always bending back after a moment to make way for the other. The eight large tentacles are used in a more or less regular sequence, and in general it may be said that the one which has been out of the mouth longest and which is farthest from the tentacle which is emerging will be the next to enter the mouth. They are seldom used in the exact order one would expect from this statement however. For example, those nearest the muddy bottom are usually more frequently used than the others. Many observations were made as to the sequence in the wiping of
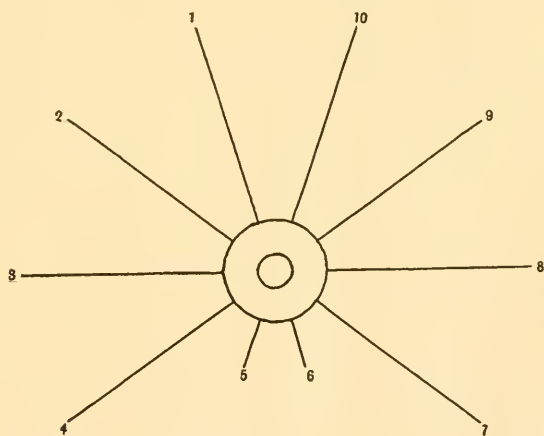

FIG. 3. Diagram to show the arrangement of the tentacles around the mouth as seen in an anterior view.

the tentacles and the following series is a typical one (see Fig. 3): 2, 7, 1, 4, 10, 8, 3, 9; 7, 2, 1, 4, 10, 8, 3, 9; 2, 7, 1, 4, 10, 8, 3, 9; 7, 2, 4, 1, 7, 10, 3, 4, 8; 2, 7, 9, 1, 3, 9, 7, 1, 8, 3, 10, 2, 8, 1, 7, 4, 8, 3, 10, 2. In this series a rather regular se-

quence is shown in the use of the tentacles.   Number 7 was used eight times ; numbers 1, 2, 3, 8, seven times ; numbers 4 and 10, six ; and number 9, five times.   The time required for the fifty-three reactions was nine minutes and thirty seconds.   A little over ten seconds was therefore required for the wiping of each tentacle.   No account was taken of the two ventral tentacles in this series as they kept moving in and out almost constantly and without any apparent relation to movements of the others.   In another larger series the different tentacles were used the follow-ing number of times : No. 1, twenty-one ; No. 2, sixteen ; No. 3, fourteen ; No. 4, twelve ; No. 7, eleven ; No. 8, fourteen ; No. 9, twenty-one ; No. 10, nineteen.   In this case tentacles 1, 10 and 9 were nearest the surface of the sand and they were used most frequently while those on the opposite side of the mouth (3, 4, 7) were less often employed.   The time for this series of one hundred and twenty·eight reactions was fifteen min-utes and thirty seconds, seven and a quarter seconds being re-quired for the wiping of each tentacle.

The feeding reaction usually occurred only after an individual had been undisturbed for some time and when it was partly buried in the mud or sand, but animals were sometimes observed to feed when attached to the side of a jar.   No stimulus was found which would cause *Thyone* to extend the tentacles and feed.   Attempts were made to induce animals to perform the feeding reaction by allowing crab or fish extract to flow gently over the anterior end ; and by using mud from the place where they were collected, but such stimuli were without results or caused only the withdrawing reaction.   In one instance, how-ever, a positive reaction was observed.   In this case a small por-tion of a bryozoan colony (*Bugula*) was dropped in such a way that it fell upon the anterior end of a partly buried individual. The tentacles were at once extended and the anterior end of the body was bent over so that they scraped the point where the stimulation had occurred.   This experiment was repeated many times and on different individuals but no other positive reaction was induced.   From these observations it may be concluded that the feeding reaction occurs only after the animal has been undis-turbed for a time and is probably brought about mostly by inter-nal factors, such as hunger.

Thyone's food consists of the microscopic organisms and debris to which the tips of the branching tentacles adhere. Such materials are wiped off as the tentacles are thrust into the mouth and extended again. The stomachs of seven freshly collected individuals were examined on August 10 and found to contain : living protozoans (*Lichnophora*, *Gymnodinium*), nematodes and diatoms (several species) ; filamentous and unicellular algæ ; pieces of plant tissue ; encysted protozoans ; two harpacticid copepods ; and an ostracod. *Thyone* is apparently a rather indiscriminate feeder but sand was infrequent in the stomach contents and, though particles of sand were seen sticking to the tentacles as they entered the mouth, most of them were brought out again as the tentacles emerged.

VI. RESPIRATORY MOVEMENTS.

Thyone carries on a regular system of breathing movements by which water is taken into the cloacal chamber and expelled again. The general plan of this chamber is shown in median longitudinal section in Fig. 4. There are three openings from
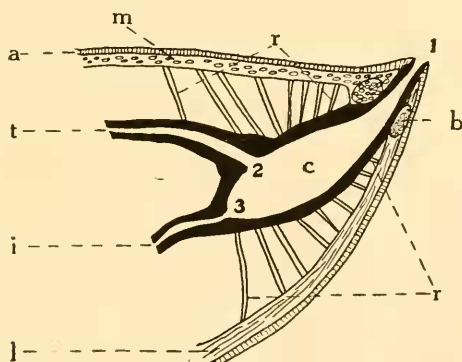

FIG. 4. Diagram representing a median longitudinal section through the posterior end of the body. *a*, integument; *b*, sphincter muscle ; *c*, cloacal chamber ; *i*, intestine ; *l*, longitudinal body muscle ; *m*, circular body muscles ; *r*, radial muscles ; *t*, respiratory trees. *1*, opening into cloacal chamber ; *2*, opening into respiratory trees ; *3*, opening from intestine.

the cloacal chamber *c*. These lead to the exterior *1*, to the respiratory trees *2*, and to the intestine *3*. During respiration the opening from the intestine *3* into the cloaca usually remains closed and takes no part in the breathing movements. Water is

drawn into the cloacal chamber by closing the opening to the respiratory trees *2* and contracting the radical muscles *r*, which extend from the cloaca to the body wall. The cloacal opening *1* is then closed, the respiratory tree aperture *2* is opened, and the contraction of the walls of the cloaca forces the water into the respiratory trees. Sometimes the cloacal opening *1* is kept closed while the water is forced back and forth from the cloaca to the respiratory trees, but the water is usually expelled from the body after each inspiration. When an individual is placed in shallow water so that the terminal opening *1* is just below the surface, the water is often expelled with enough force to form a fountain-like " spout " 3 or 4 cm. high.

The rate of the spouting reactions varies considerably, as is shown by the following observations, made upon two individuals which were buried in the sand. The average time between 144 consecutive spouting movements was 39 seconds for one animal ; and the average time between 24 spouts was thirteen seconds for the other. In order to ascertain what would happen if these two individuals were prevented from spouting for a long period of time, they were first observed as they lay buried in the sand and the rate of their normal respiration noted. They were then made to pull the posterior end down into the sand by poking it with a glass rod, and whenever it started to emerge it was poked so that it was again withdrawn. The first animal spouted every twenty seconds (seven times) before being prevented from breathing and was then kept under the sand for one hour and twenty minutes. After the posterior end had appeared again there were no spouting movements for four minutes, and the next seven spouts averaged 36 seconds apart. The other animal averaged thirteen seconds between 24 spouts before its breathing was prevented. It was kept under the sand for two hours, 36 minutes and forty seconds ; and at the end of that time it spouted with the posterior end still buried in the sand. The next nineteen spouts averaged one minute and five seconds apart. In both these instances the rate of respiration was more rapid before the breathing movements were prevented than afterwards. That is, an individual breathed more slowly after it had been made to " hold its breath " for an hour or two than it had before. This result can be accounted

for by the fact that the movements which force the water into the respiratory trees were more forcible after the period passed without respiration and hence they required a longer time. In addition to the respiratory movements described there is doubtless an exchange of gases through the integument and *Thyone* could probably exist for some little time without spouting.

VII. Responses to Stimulation.

Having completed the consideration of locomotion, feeding, and respiration, attention will now be directed toward some of the responses which result from such forms of stimulation as can be controlled by the experimenter.

1. *Tactile Stimulation.* — *Thyone* is extremely sensitive to contact with solid objects. If an animal is twisting about on the surface of the sand and comes in contact with a solid surface, the tube-feet are immediately extended and attached. Furthermore, if an individual is placed in a glass dish, it comes to rest in the angle between the bottom and side, where the body has the greatest surface in contact. When the contact stimulus is received from a moving object, the characteristic withdrawing reaction is given and the response varies with the stimulus. The tip of a glass rod may be gently pressed against the side of an individual if the movement is very gradual but the same pressure will cause a marked response if suddenly applied. The following experiment is a good example of sensitiveness to jars and other slight disturbances. A drop of water was allowed to fall from a height of one meter into a one-liter beaker containing a feeding individual. As soon as the drop struck the surface of the water above the animal, the tentacles were withdrawn and the cloacal opening was closed.

There is great variability in the sensitiveness of different individuals and those which had been in the laboratory for some time often allowed the tentacles to be touched with a glass rod whereas freshly collected individuals would contract at any slight jar, such as the closing of a door. Grave (:05) obtained similar results from his study of *Cucumaria*.

2. *Gravity.* — *Thyone's* responses to gravity were tested in two ways, by the righting reaction and by locomotion on an inclined

surface. The righting reaction is one of the most characteristic activities of this species. If an individual is placed in a flat-bottomed dish containing sea water and held with its ventral side uppermost until the tube-feet have attached themselves (usually about half a minute), it slowly pulls the body over with the tube-feet until the ventral surface is against the bottom of the dish. The tube-feet are helped to perform this righting reaction by the rings of muscular constriction which pass slowly from one end of the body to the other. The direction of the turning is determined by various factors, light being an important one. For example, when an individual rests on its dorsal surface with the long axis of the body at right angles to the direction of the light, the ventral surface is usually turned away from the light as the body is righted.

In order to test the locomotor reactions on an inclined surface four individuals were each given four consecutive trials in the
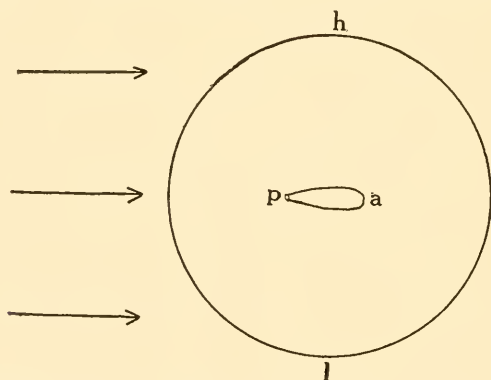

Fig. 5. Diagram showing the position in which individuals were placed in the dish during experiments to test the locomotion on an inclined surface. The arrows represent the direction of the light. *a*, anterior end ; *h*, high side of dish ; *l*, low side of dish ; *p*, posterior end.

bottom of a round glass dish, which measured thirty centimeters in diameter and contained sea water. This dish was placed directly in front of a window which was the only source of light in the room and the bottom was tipped 5.6° from the horizontal at right angles to the direction of the light rays. Animals were placed separately in this dish with the long axis of the body parallel to rays of light (Fig. 5). They were first given two trials with the bottom of the dish

inclined toward the left, the anterior end of the body being placed toward the window in the first case and away from it in the second. The dish was then inclined toward the right and the same procedure repeated. The distance from the center to the edge of the dish was fourteen centimeters and directions which the different individuals took in reaching the latter are shown in Table I. These results do not show any strongly geotropic tendency and the next step would naturally have been to test individuals on an inclined surface with the light coming from above or to make similar tests in total darkness but lack of time prevented such experiments being carried out.

TABLE I.

Deflection in moving fourteen centimeters away from the light on a plane surface inclined 5.6° at right angles to the direction of the light rays.

Direction of Locomotion.	Straight away from Light.	Up Incline.	Down Incline.
Individual No. 1...........................	+	10° 10°	5°
Individual No. 2...........................	+	90° 10°	90°
Individual No. 3...........................	+ + + +		
Individual No. 4...........................			10° 22° 10° 5°
Total reactions...........................	6	4	6
Average deflection...........................	0	30°	24°

3. *Chemical Stimuli.* — No extensive experiments to test reactiveness to chemical substances were made. It was hoped, however, that positive responses might be obtained by using food substances, but repeated experiments with fish and crab extract, crushed eel-grass and scrapings from the surface of the mud were without results. The reactions which resulted when the water became foul were doubtless due to chemical stimuli. In this case individuals extended the posterior end of the body until the cloa-

cal opening was near the surface of the water, or came out of the sand and climbed up the side of the jar in which they were kept, or increased the size of the body and ceased to respond to shadows and other slight stimuli, and in some cases even cast out the visceral organs.

4. *Change in Density of Medium.* — *Thyone* can stand a marked increase or decrease in the density of the water in which it lives without serious interference with its activities. In order to test the effect of increased density an individual was placed in a one-liter beaker which had sand in the bottom to a depth of six centimeters. This beaker was filled with sea water and allowed to remain on the table in the laboratory from July 12 until August 7 (twenty-five days), when the animal died. During this time the water had evaporated so that the specific gravity had increased from 1.024 to 1.052. This animal showed no signs of the changes due to unfavorable environment until July 1, when it came out of the sand where it had been previously buried and lay on top. From this time it began to show signs of degeneracy, the skin was blistered off in spots and the body took on a peculiar elongated form. Many of the reactions continued to be normal however and the usual shadow reaction (which is described in the next section, p. 277) was easily induced the day before it died. On the morning of August 7 the animal failed to respond to shadows but gave the withdrawing response when it was poked gently. Four hours later it was dead. Subsequent examination showed that the visceral organs were still in place and had not been cast out on account of the increased density of the water.

The effects of a decrease in density were next investigated. Individuals were placed for a time in various mixtures of sea and fresh water. They were then returned to sea water and their subsequent condition noted. The results of these experiments are shown in Table II. No individual ever attempted to burrow while it was in a solution of lesser density than sea water, although sand was always placed in the bottom of the dish. The body remained contracted, spouting was infrequent and the tube-feet were never attached and seldom even extended over much of the body surface. In the cases where the animals survived their immersion in the mixtures they soon began regular spouting move-

ments after being replaced in sea water and gave typical, burrow-
ing, feeding and shadow reactions within a few hours.   The vis-
ceral organs were cast out in only one case and that was after an
individual had been left in perfectly fresh water for three hours.

TABLE II.

Results of experiments in which *Thyone* was placed in mixtures of fresh and sea
water.

Parts, by Volume, used for Mixture.		Number of Individuals Used.	Time Left in Mixture.	Condition after the Experiment.
Sea Water.	Fresh Water.			
1	1	1	3 hours.	Good.
1	2	2	1 hour.	Both good.
1	2	2	4 hours.	Both good.
1	2	2	24 hours.	Both good.
1	3	2	1 hour.	Both lived, but were in poor condition.
1	4	3	Until dead.	Died in 5-6 hours.
0	1	2	3 hours.	Recovered somewhat, but died within 3 days.

As will be seen from the table, animals which were left for
twenty-four hours in a solution which consisted of one third sea
water and two thirds fresh water, were apparently uninjured ;
while individuals which were immersed in fresh water for three
hours died.   Mr. E. D. Congdon's observations on this species are
of interest in this connection.   He told the writer that he had found
Thyone briareus at the mouths of rivers in water which was half
salt and half fresh, as judged by the specific gravity, but it was
never found any farther up rivers than that.

5. *Light Stimulation.* — *Thyone* is extremely sensitive to a de-
crease in the light intensity and what may be called the " shadow "
reaction is one of its most characteristic responses.   If an in-
dividual is resting quietly in the sand with only the posterior end
of the body exposed and the experimenter's hand is passed be-
tween it and the window, it at once withdraws the visible portion
of the body.   This response is of course variable and it may not
occur at all or it may be so pronounced that the animal com-
pletely disappears beneath the sand.   The same withdrawal is
induced if a shadow is thrown on the anterior end or even on one
tentacle and a particularly sensitive individual was caused to con-
tract by extending a pencil over the top of the beaker in which it lay.

Although such characteristic responses are given when the light intensity is decreased no reaction occurs when there is a corresponding increase. An individual will contract at once when an object is interposed between it and the light, but it gives no response if the object is removed after a time. Furthermore, when light from a large oil lamp or from the sun was suddenly reflected from a mirror on a feeding individual there was no response. This sensitiveness to decrease in the light intensity and lack of response to an increase is similar to the reactions observed by Hargitt (:06) in *Hydroides dianthus* and other annelids. Uexkull ('97) has also described striking shadow responses in sea-urchins.

Thyone gives well-marked locomotor responses to light which may be illustrated by the following experiment : Eight individuals were successively placed in a shallow rectangular glass dish which measured 29 cm. long by 25 cm. wide, and contained sea water. The dish was enclosed in a black box which had an opening at one end. This opening was directed toward the window so that light was admitted from only one direction. The animals were always placed with the long axis of the body at right angles to the light rays and the direction of the subsequent movement was then observed. In a series of twenty-four reactions the locomotion in every case carried the animal away from the light to the end of the dish, but there was no definite orientation of the body in relation to the light. In ten of these negative responses the anterior end was ahead as the individual moved ; in nine instances the posterior end preceded the anterior ; and in five the locomotion was straight toward the right or left. Not one of the eight individuals moved in every case with the anterior or posterior end in front.

The influence of the negative light response is also apparent in the righting reactions. When individuals were placed in the same position as in the experiments described in the last paragraph, except that the ventral side of the body was uppermost, the righting reaction usually carried the ventral surface away from the light. Two individuals were given fifteen trials each in the manner just described, the anterior end being turned alternately toward the right and left in successive trials. One of them turned four times toward the light in righting itself and

the other turned only three times in that direction. In other words, twenty three out of thirty reactions (77 per cent.) were away from the light.

Another reaction which shows a negatively phototropic response is apparent when an animal burrows next the side of a glass vessel. It never remains against the glass but moves out into the sand after it has covered itself. This action is without doubt due to light stimulation for an animal will remain indefinitely in contact with an opaque object, such as a stone.

These reactions show that the *Thyone* is sensitive to decreased light intensity, and that it is negatively phototropic but without any definite orientation of the body to the source of the illumination, or the direction of the rays. This lack of orientation is rather striking in a bilaterally symmetrical animal and it shows that the response is not brought about in this case by unequal stimulation on the right and left sides of the body.

6. *Heat Stimulation.* — *Thyone* was not found to be very responsive to temperature changes, and individuals lived for several days at room temperature (24–28° C.) without apparent injury. Attempts were made to induce reactions by local changes in the temperature. The method was to siphon boiling water or a mixture of ice and salt water through a small U-shaped glass tube which could be brought close to the surface of the individual to be tested. Although six different animals were each tried twice with the hot tube and twice with the cold tube by holding the tube less than a millimeter below the extended posterior end, not a single response was observed.

Attention was next turned to the effects of an increase or decrease in temperature which affected the whole body. To test the effect of increased temperature six individuals (which were buried in the sand at the bottom of separate beakers containing sea water) were placed two at a time on a sand-bath and slowly heated. All the animals became active after the temperature had reached 30° C. The tube-feet were waved about on all sides and the body began to execute irregular twisting movements which continued until the temperature was lowered again. Two of the individuals were slowly heated to 36.5° C., the time required to reach that temperature being one hour and thirteen

minutes. One of these animals soon died but the other was in excellent condition four days afterward. Two other animals were heated to 41° C. during two hours and thirty-eight minutes and both of them died, although one continued to contract slowly when poked for two days. The two remaining individuals were heated to a temperature of 37° C. during two hours and forty minutes. Next day they were both in excellent condition and gave good burrowing and shadow reactions.

In order to test the effect of decreased temperature, beakers containing buried individuals were placed in a pail of cracked ice and salt and allowed to remain until the temperature had been sufficiently lowered. A beaker containing one animal was placed in the " freezer " and when the temperature had reached + 8° C. it failed to give the shadow response but contracted somewhat when the beaker containing it was jarred. In two hours and twenty minutes the sand was frozen solid and covered over with ice crystals. A thermometer held against the body of the animal registered — .5° C. At this temperature the posterior end still contracted when poked. Twenty minutes later with the temperature at — 1.6° C. only a feeble contraction was induced by poking, and after thirty minutes more the whole body was stiff and apparently frozen solid. The animal was left an hour longer and became completely covered over with ice crystals. The beaker was then removed, after having been in the freezer four hours and twenty minutes. The animal was found to be dead after the ice thawed. Another beaker which contained two *Thyones* was introduced into the freezer. Both these individuals were buried in the sand and covered by sea water. The temperature was reduced so that the sand was frozen and a thermometer resting against one of the animals registered — 2° C. to — 3° C. for two hours and forty minutes. After having been in the freezer three hours and forty minutes the beaker was removed. Twelve hours later both the individuals it contained had cast out the viscera but they did not die and continued active for several days, though they were in poor condition and gave no shadow reaction. Grave (:05) observed that *Cucumaria* retracted the whole body during cold weather and Mr. George Gray had informed me that *Thyone* buries itself six or eight inches in the sand

during the winter. I had therefore expected to see the burrowing reaction take place as the temperature was reduced but all three of the individuals remained perfectly quiet as the ice formed around them and the posterior end was not withdrawn.

From the experiments described it is evident that *Thyone* is comparatively insensitive to thermic changes and that it is able to react through a wide range of temperatures. The maximum and minimum vital limits are in the neighborhood of 40° C. and 0° C. respectively.

VIII. Experiments to Determine whether the Integrity of the Nervous System is Essential to Reactions.

The classical work of Romanes ('85) showed that a single fifth of the body wall of a sea-urchin was able to carry on locomotion without any of the visceral organs. Such fragments executed righting reactions and showed the same positive phototropism which was characteristic of entire animals. Mead (:01) kept detached starfish arms alive for as much as three months and they retained their powers of locomotion and gave the usual righting reaction. Von Uexkull ('97) found that pieces of sea-urchin would react to mechanical stimulation but the responses to shadows depended on keeping the system of radial nerves intact. These and other observations show that the nervous system of the asteroids and echinoids is little centralized in some respects, though Jennings (:07) has recently described some remarkable instances of association in the starfish. Clark ('99) found that cutting the oral nerve ring made no appreciable difference in the reactions of *Synapta*. Henri (:03, :03*a*, :03*b*) showed that nerve centers exist in the radial nerve trunks of *Stichopus regalis* and that reflex muscle contractions could be induced through them by stimulating the skin. He states that such radial nerve centers control only a limited portion of the body musculature and that reflexes which involve more than one of the longitudinal muscles must pass through the oral nerve ring.

As has been stated, the nervous system of holothurians consists of a circum-oral ring which gives rise to five radial nerve trunks and these are connected through their finer branches which anastomose to some extent. This system has been modified some-

what to conform to the bilateral plan of structure and, as the radial nerves are not equally well developed, there is a dorso-ventral as well as an antero-posterior differentiation. In order to test the reactions of fragments of the body a series of experiments was carried out in which twelve *Thyones* were each divided into two approximately equal pieces by a transverse cut. The two pieces of each animal were laid in a dish of sea water before a window in the position shown in Fig. 6. The ventral side of
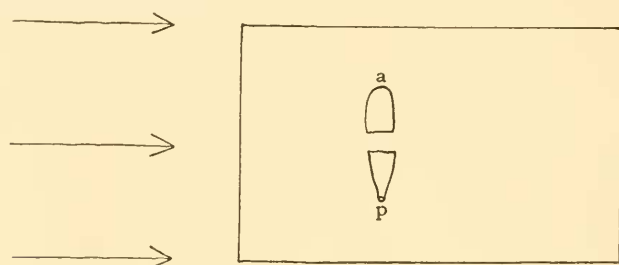
FIG. 6. Diagram to show the position in which animals were placed in the dish after being cut in two. The arrows represent the direction of the light. *a*, anterior end ; *p*, posterior end.

the body was always placed uppermost and the long axis of the body was at right angles to the direction of the rays of light. The movements of the two halves were observed during the three hours following their separation and a summary of these reactions is given in Table III. Although the tube-feet were more or less

TABLE III.

Showing the number of anterior and posterior halves of twelve *Thyones* which gave different reactions.

Nature of Reaction.	Locomotion.				Righting.	Shadow.
	Toward Light.	Away from Light.	Straight Ahead.	None.		
Number of anterior halves reacting..................	3	2	2	5	11	3
Number of posterior halves reacting..................	4	7	0	1	12	9

active on both halves of the body in all cases, it will be seen that the posterior halves gave characteristic reactions more often than the anterior portions. They carried on normal spouting move-

ments and performed the righting reaction more rapidly than the anterior halves. The only response in which the anterior half approached the posterior in the number of individuals which responded was in the righting reaction. This was probably due, in part at least, to the structure of the tube-feet which have more efficient sucking discs on the ventral than on the dorsal surface, and those on the ventral side would hence be more likely to become attached if all of them were active. Two of the individuals were kept in a dish without changing the water for three days after they had been bisected. Both the posterior halves remained in good condition and gave characteristic shadow responses at the end of the third day, but both the anterior portions threw out the viscera during the second day and were dead on the third day.

These experiments show that the presence of the circum-oral nerve ring is not essential for the performance of correlated reactions and that the posterior half of the body is apparently able to carry on movements better than the anterior. This greater efficiency shown by the posterior end of the body is perhaps what might be expected from the fact that the whole anterior portion is often cast off and dies while the posterior end lives and regenerates the lost organs. These conclusions do not agree with those reached by Henri (:03b) from his work with *Stichopus regalis*. He believed that the oral nerve ring was necessary for general muscular reflexes.

IX. Variability of Reactions.

Few of the reactions which have been described in this paper could always be induced by a repetition of a stimulus which had previously brought them about. The response which was perhaps the most unfailing was the contraction of the body which resulted from gentle mechanical stimulation with some pointed object, but even this response varied with the strength of the stimulus, the condition of the individual and other factors. Not only did characteristic responses often fail to take place after a stimulus but they were sometimes modified so that they did not take place in the usual manner. Such differences in reactions may be due to internal causes which have to do with the structure or the past experience of the individual, or they may be caused by various

external factors. It is important to discover, if possible, what stimuli will cause these differences in behavior. When *Thyone* extends its tentacles and feeds, the movements are brought about by such factors as hunger, or the presence of food, or by a combination of two or more such stimuli. If we throw a shadow on it as it feeds, the tentacles contract and the withdrawing reaction takes place. Although all the stimuli which were effective in producing the feeding reaction but a moment ago are present and acting, we have introduced an additional stimulus which has modified the response. This is an example of inhibition, as the presence of one stimulus inhibits the response to certain other stimuli. The periodic repetition of a stimulus is another means by which responses may be changed. As Jennings (:05) says of this method " the physiological state tends to resolve itself into another and different state " after a stimulus has been received. An individual will be in a different condition, and will really be a different animal, after it has received the first stimulus and may therefore give a different response the second time the same stimulus is received. Some of the instances of variable behavior which were observed will now be briefly considered.

1. *Repetition of a Stimulus.*— Responses usually vary in degree when a stimulus is repeated at regular intervals. If an individual is touched gently with a glass rod and then touched again on the same spot at one minute intervals the withdrawing response which was at first marked becomes gradually weaker and finally ceases altogether. Similar results may be obtained by allowing a drop of water to fall at regular intervals into the dish which holds an animal, or by periodically throwing a shadow upon an extended individual. By increasing the interval of time between successive stimuli a larger number of responses may be obtained but the result will be the same in the end. Individuals which have been newly brought from the ocean contract at the slightest disturbance and give the withdrawing reaction whenever anyone walks across the floor or opens a door or when any other slight change occurs in their surroundings, but they soon cease to respond to such stimuli. For example, one individual which had been kept for two weeks on a table in the laboratory carried on normal feeding and breathing reactions while people were con-

stantly passing between it and the window. After this animal had been allowed to remain in a quiet situation in another room for a week however it had again become extremely sensitive to shadows, jars, currents of water and other gentle forms of stimulation.

Thyone sometimes modified its behavior after a stimulus had been repeated several times and a new form of response occurred. On one instance an individual which had been used in previous experiments was stimulated by gently sticking a glass rod among the tentacles as it was feeding. At first all the tentacles were withdrawn as soon as the rod touched one of them, but after the fourth trial they were no longer retracted, and when the rod was pressed gently against the mouth the anterior end was turned to one side but not withdrawn. This change in response was brought about in half an hour.

2. *Inhibition.* — As has been stated, the shadow reaction was one of *Thyone's* most constant and characteristic types of response but it would not take place if certain stimuli were present. To give some specific instances : This reaction was inhibited when the temperature of the water fell below 10° C., when the posterior end was greatly elongated toward the surface on account of stagnant water, and after the respiratory movements had been prevented from occurring for some time. In all these cases individuals gave characteristic shadow responses before and after the inhibiting stimulus was present. Another characteristic reaction was locomotion away from the light, but, when an animal was against the side of a glass vessel it often moved at right angles to the direction of the light rays, the thigmotactic stimulus being more potent than the light. Furthermore, if an individual was laid on its dorsal surface with the median plane inclined slightly toward the source of the illumination, it often moved one or two centimeters toward the light in righting itself. These instances are typical of others which might be given and they show that though *Thyone's* responses are largely of a stereotyped nature, they are interrelated in such a way that one may inhibit another.

X. General Considerations.

Thyone briareus is a holothurian which is rather strikingly adapted to a sedentary life. It is not able to change its place of abode easily and it is hence highly resistant to unfavorable conditions in its environment. Individuals which were allowed to lie on moist sand exposed to the air for eighteen hours were apparently uninjured. This tenacity to life is also shown by the ability this species manifests to withstand changes in the temperature and the density of the water in which it lives. The methods of feeding, locomotion, respiration and other activities are adapted to the peculiar conditions under which it exists. Passing most of its life buried in the mud, *Thyone* probably does not often fall a prey to large enemies but it is protected from them by the withdrawing reaction, by its locomotion away from the light and by its habit of pulling pieces of eel grass and other debris over the body.

Many of *Thyone's* movements show a lack of correlation. In ordinary locomotion on a solid surface, the tube-feet which are behind are often forcibly pulled loose from their attachments instead of being released by means of some impulse from the central nervous system. Such organs as the tube-feet are able to work more or less independently, but they may also be actuated by a unified impulse, as is shown when they are simultaneously extended or contracted over the whole body and the same unity is apparent in their action as they pull the animal along in a definite direction. On the other hand many reactions show considerable power of correlation and adaptation. Correlation is shown in the use of the circum-oral tentacles, as they move in a rather definite order. Very often, however, two of them endeavor to enter the mouth at the same time, but one always bends aside to make way for the other. If the correlation in the movements was perfect in this case, two tentacles would not try to enter the mouth at once, and if there was no correlation they would struggle with each other indefinitely. Furthermore, when a feeding individual lies on its side, the tentacles which scrape the bottom are used oftener than the others and there is thus an increased chance of obtaining food.

Generally speaking, it may be said that *Thyone's* behavior,

like that of other sedentary animals, is mostly made up of stereo-typed reactions which occur regularly in response to certain stimuli. Furthermore, many of these reactions are carried on independently by certain separate organs and two parts of the body may "work against each other" for a time, but, under the proper conditions of stimulation, all these simpler reactions may be unified into one general correlated response. Although the reactions are largely stereotyped in nature they may be changed by experience or inhibited by the presence of different stimuli. The stereotyped methods of response are usually adequate to meet the conditions under which *Thyone* exists and would usually enable it to survive in the struggle for existence. If they are not adequate, however, they may be modified to meet new con-ditions. For example, this species usually burrows into the mud so that only the posterior tip of the body is exposed and even this is withdrawn if the slightest shadow falls upon it or if the water is agitated. If the water becomes stagnant the same individuals that were formerly so reactive will climb up the side of the jar and cease to respond to such slight stimuli as shadows and water currents, and they contract only when touched by some solid object. As the water becomes foul, the greatest need of the organism is oxygen and the behavior described would enable this to be obtained, but to accomplish this end, the animal would be obliged to forego the temporarily less important matter of protection from its enemies.

When compared with an echinoid or a star-fish as described by Romanes ('85) and Jennings (:07), or with an ophurian as it is represented by Glaser (:07) *Thyone* falls short in the range and diversity of its reactions. This is probably due in part to its sedentary mode of existence and the study of holothurians which do not burrow might show a somewhat different set of reactions. Perhaps the most interesting point which is brought out in the study of *Thyone's* behavior is the fact that, although the symmetry is so strikingly bilateral, the locomotion is carried on with the same lack of orientation which is so characteristic of other groups of echinoderms.

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THE INTERLOCKING MECHANISMS WHICH ARE FOUND IN CONNECTION WITH THE ELYTRA OF COLEOPTERA.

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It is a matter of common knowledge that the elytra of most beetles are co-adapted with each other and with the body of the insect. Yet it appears that no one has ever described these co-adaptations in any detail in spite of the fact that several very interesting mechanical devices are here brought into use. The attention of the senior author of this paper was called to them while studying the muscular system of beetles. At that time he discovered that a small muscle, attached to the meta-episternum, had been erroneously thought to be an expiratory muscle and that in reality it operated a mechanism for hooking the edge of the elytron to the body at this place (Breed, :03, page 332).

Writings on the subject seem to be limited to a few general statements in text-books. Packard ('98) says that the wing cases of beetles join along their dorsal suture like the valves of a mussel shell. He further states that there is an interlocking of the elytra with the scutellum, citing the stag-beetle as an example. He also finds that the elytra of stag-beetles interlock with each other by means of a groove, and that this is the method usually found in beetles; but that in some cases the joining is after the method of two cog-wheels. He likens these devices to the two methods most used by the cabinet-maker in joining boards.

Sharp ('99) says that in most beetles the elytra are fitted together and to the sides of the body, except at the tip, but he gives no further explanation. He also states that sometimes the tips of the elytra are fastened to the body, but that this occurs only in the cases where the abdomen is not entirely covered by them. He says further that in the blister beetles, which include the Cantharides and the Meloides, the elytra are not co-adapted with the abdomen. The former are winged but the latter are so-called

apterous forms, with elytra overlapping at the base. The same author says that in some species the elytra are soldered together along the suture. The degree of firmness of the joining varies even in specimens of the same species, probably depending on the age of the individual.

1. MATERIAL AND METHODS.

The material used was *Lachnosterna fusca* Auct., the June-bug or May-beetle, *Thymalus marginicollis* Chevr., a small beetle which lives in the common shelf fungus of white birch, and *Tenebrio molitor* Linn., the meal beetle.

The method used in examining the co-adaptations of the elytra in the two larger beetles was to take specimens hardened in alcohol and cut off the posterior part of the body, wings and elytra with a razor. Then the remainder of the insect was placed under a low power of the microscope in such a position that the face of the cross section could be viewed. In some cases it was found advantageous to embed the whole beetle in paraffin first. Then the desired section was cut free-hand with a razor, after which a part or the whole of the paraffin was dissolved away and the cut face examined with a microscope. When studying the separate elytra, thin sections were cut in pith in the same way that botanical sections are so often prepared. In this way perfect, though rather thick, sections were obtained, whereas microtome sections were badly broken.

In the case of *Thymalus*, which is a small beetle with a comparatively thin cuticula, it was found possible to prepare series of microtome sections of the entire insect. These series show both the interlocking along the dorsal suture and the musculus episternalis with its related parts. By selecting young imagines of *Lachnosterna* and *Tenebrio* and sectioning only a portion of the body, series of microtome sections of these beetles were prepared which show the musculus episternalis and its related parts.

2. OBSERVATIONS.

There are commonly found in beetles four devices for fastening the elytra in place, all of which may be utilized in one animal. The fastening may be accomplished :

1. By a co-adaptation of the elytra along the dorsal suture.

2. By means of a groove on the dorsal face of the metathorax into which the swollen inner edges of the elytra fit.

3. By slipping the anterior edges of the elytra under the scutellum and hooking them (*a*) on to the scutellum, or (*b*) on to the metathorax. Pressure derived from the retracted prothorax may aid in keeping these edges in position.

4. By hooking the anterior lateral edges of the elytra over ridges or into grooves on the lateral faces of the metathorax.

(*a*) *Interlocking Mechanisms found in Lachnosterna.*

Lachnosterna fusca is one of the lamellicorn beetles. The head, prothorax and elytra show in dorsal view, together forming a broad oval outline. The elytra almost cover the abdomen, the exposed part being curved downward in such a way that it cannot be seen from above. The abdomen is shortened and rounded, and the elytra curve sharply downward at the sides and posteriorly.

The first three of the methods of interlocking mentioned above are used in *Lachnosterna*. The hooking mechanism of the fourth method is present, but is not functional.
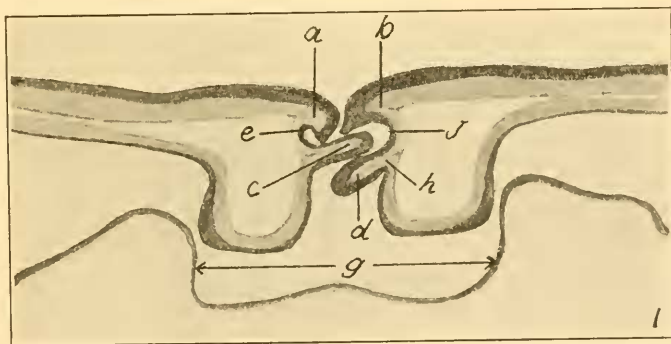
FIG. 1.   Mid-dorsal portion of the cross section of the elytra and metathorax of *Lachnosterna*, showing the adaptation of the elytra to each other along the dorsal suture and to the metathoracic groove. $\times$ 75.

1. The method of joining along the dorsal suture is shown in Fig. 1, which represents a cross section of the mid-dorsal region of the elytra. In this case the elytra are nearly as they would be when the elytra were firmly closed, and are partially slipped into

the underlying metathoracic groove.   When the elytra are separated, the cross section of the right one appears as in Fig. 2. The ridge *b* is stiff, but the ridge *d*, being narrower at *h*, acts like a spring.   When the two elytra are drawn together, the ridge *c* strikes the ridge *d* and bends it downward.   The ridge *c* then
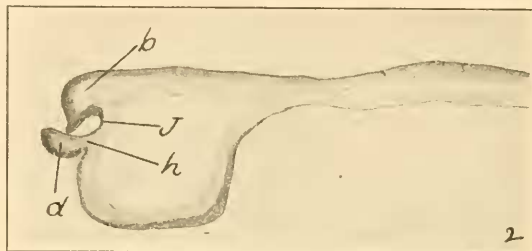

FIG. 2.   Cross section of the mid-dorsal portion of the right elytron of *Lachnosterna*, showing the relation of the two ridges when the two elytra are not locked together.   ✕ 75.

slips into the groove *j*, and *d* springs back, holding *c* tightly in the groove *j*.   By comparing Fig. 2 (a figure of the right elytron) with that of the left elytron represented in Fig. 1, it will be seen that the two are remarkably alike when the elytra are separated. No conception of the way in which they interlock was formed until the two were studied in their natural relations by the method
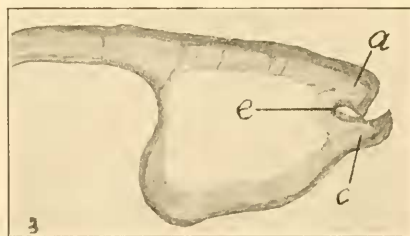
FIG. 3.   Cross section of the mid-dorsal edge of the left elytron of *Lachnosterna* as seen in the extreme anterior portion.   ✕ 75.

described above.   The ridges and grooves along the dorsal suture have essentially the same form throughout the length of the elytra but the joining is the firmest along the anterior third of the suture.   Figs. 3 and 4 represent the region close to the point of the scutellum.   Figs. 1 and 2 show the structure at a point

about one millimeter back of the scutellum.   Figs. 5 and 6 show
cross sections of the elytra from near the middle region.   In all
of the specimens examined, the ridge on the left elytron hooks
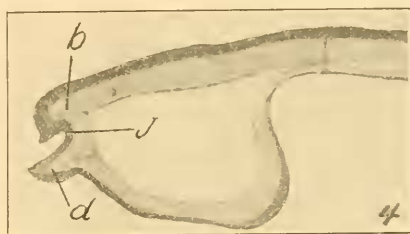into the groove on the right elytron.

FIG. 4.   Similar to Fig. 3.   Right elytron. $\times 75$.

2. Figs. 1 to 6 show the thickenings of the lower face of
each elytron along the mid-dorsal edge in cross section.   Figs. 1
and 2 show the form of these thickenings in the metathoracic
region.   Beneath these thickenings there is a groove along the
metathorax, well stiffened with chitin, into which the thickenings
fit tightly when they are interlocked.   This groove is seen in
cross section at g, in Fig. 1.   The thickenings of the elytra in the

FIG. 5.   Cross section of the mid-dorsal thickening of the left elytron of *Lach-
nosterna* as seen near the posterior end of the elytron. $\times 75$.

anterior part of the suture are more abrupt than elsewhere, the
contour of the under side of the elytron being here S-shaped in
cross section (Figs. 3 and 4), so that the thickenings hook into
the metathoracic groove, which is slightly wider in its ventral
than in its dorsal part.

3. The metathoracic groove widens in its anterior portion, so that the entire groove has the form of a Y with its arms projecting forward. The triangular scutellum lies in the opening between the arms of the Y. In closing the elytra, their anterior
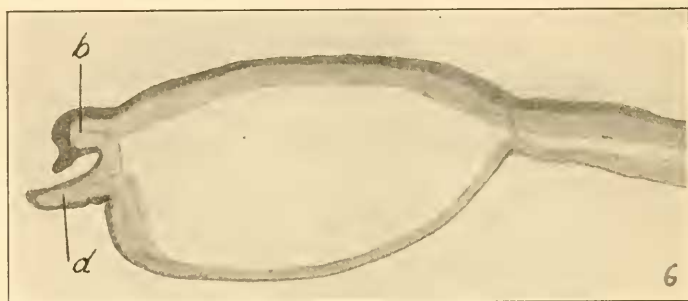

FIG. 6. Similar to Fig. 5. Right elytron. $\times$ 75.

edges slip under the diagonal edges of the scutellum and hook over the ridges made by the diverging arms of the Y. The thickening along the edge of the elytron at this point has still
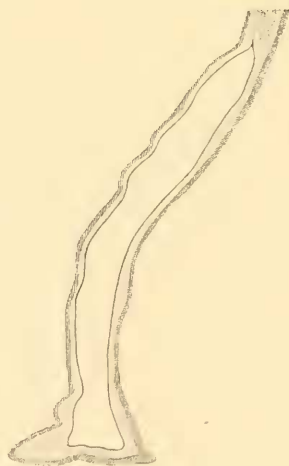

FIG. 7. Cross section of the lateral edge of the right elytron of *Lachnosterna.* $\times$ 150.

more the form of a hook than those shown in Figs. 3 and 4. The interlocking is therefore very firm in this region, especially as the downward pressure of the scutellum aids in resisting any
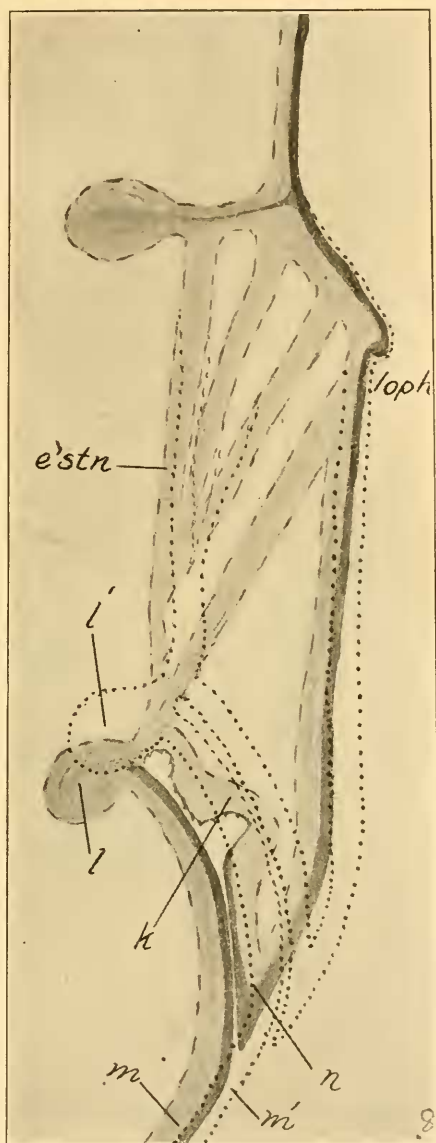
FIG. 8.   Lateral portion of a cross section of the metathorax of *Lachnosterna*, showing the parts affected by the contraction of musculus episternalis. $\times$ 150.

forcible detachment of the elytra.   This pressure of the scutellum is supplemented by the retraction of the prothorax against the

mesothorax. There is no interlocking of the elytra with the scutellum in this beetle.

4. The elytra are not fastened along the lateral faces of the metathorax, although a rudimentary hook (Fig. 7) is found along the anterior lateral edge of each elytron. A corresponding ridge hooking downward (Fig. 8, *loph.*) is found on the meta-episternum, a short distance below the origin of the musculus episternalis (*e'stn.*).

The probable method by which this hook would be operated is shown in Fig. 8. The dotted lines show the position of the movable parts when the muscle is contracted. The ridge represented in cross section at *l* is drawn up to the position *l'*, and the flexible band *k* is straightened. The meta-sternum *m* is drawn upward and outward to the position *m'*, thus forcing the ventral edge *n* of the episternum outward. A dissection of the muscular system of several beetles has shown that the lower attachment of the musculus episternalis is along a straight line, while the upper attachment is arched somewhat like the gable of a house. This form gives firmness and affords reason for believing that it is the lower attachment of this muscle which moves when the muscle contracts. Further proof of this is furnished by the triangular form of this muscle in longitudinal section (Fig. 8, *e'stn.*). Thus the dorsal end of this muscle serves as origin, while the ventral end is insertion. The movement of the ventral edge of the episternum outward would cause the slant of the ridge (*loph.*) to change slightly. If there were a functional hook present on the edge of the elytron, the change in position due to the contraction of this muscle would be sufficient to release the elytron or to allow it to return to its place.

However, since the hook present on the elytron is rudimentary, this muscle is apparently functionless though it must have been functional in some ancestral form. The muscle has not degenerated as completely as have the chitinous structures in connection with it. The degeneration of the lateral hooking mechanism may be accounted for by the highly developed interlocking mechanisms in the other parts of the body. The dorsal suture, the meta-thoracic groove, and the fastening under the scutellum furnish ample means for holding the elytra firmly in place.

(b) *Interlocking Mechanisms found in Thymalus.*

Thymalus marginicollis is one of the trogositid beetles ; it has the same general form as a lady beetle, but it is still better adapted in form of body for clinging to a surface after the manner of a limpet. The dorsal view of the body is a nearly perfect broad oval showing simply the pronotum and elytra with a small portion of the head. The flange on the edge of the elytron (seen at *f* in Fig. 9) fits closely against the surface on which the beetle is resting. The adult beetles are commonly found during the

FIG. 9. *Thymalus.* Copied from Breed, :03. Similar to Figs. 8 and 12. × 100.

early part of the summer lurking about the shelf fungi which have served their larvæ as food.

The four general methods of fastening the elytra in place which were mentioned above are all functional in this beetle. The co-adaptation between the body and the elytra is so perfect that it is nearly impossible to unclasp the elytra in a dead specimen without tearing them.

1. The co-adaptation along the dorsal suture is shown in Figs. 10 and 11. The lower ridge *d* (Fig. 11) of the right elytron fits into the groove *e*, the interlocking in this case being just the reverse of that found in *Lachnosterna* (Fig. 1). Moreover, there is no clasp arrangement, the ridge *c* remaining as rigid as the others. The suture would not hold together if there were not a lateral stress exerted upon the elytra. In the anterior region,
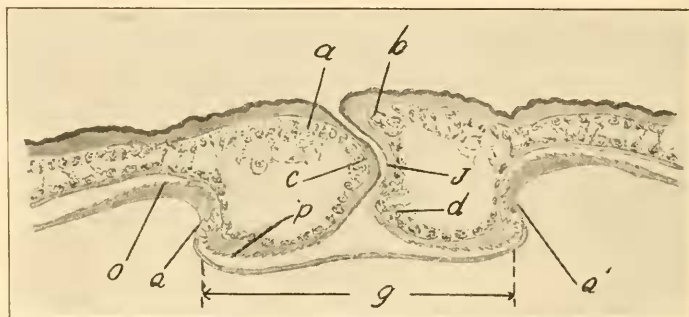

FIG. 10.   Mid-dorsal region of a cross section of the elytra and metathorax of *Thymalus*, showing the adaptation of the elytra to each other and to the metathoracic groove.   × 130.

the ridges become very feeble and in the most anterior sections (see Fig. 10) a ridge *c* on the left elytron fits into a groove *i* on the right elytron thus reversing the condition found in the middle and the posterior regions.
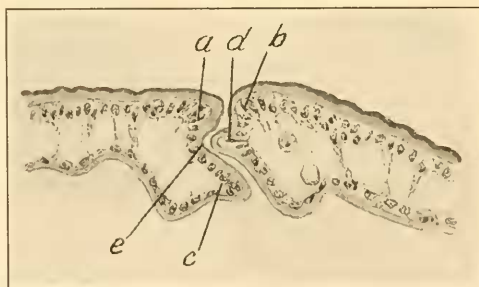

FIG. 11.   Mid-dorsal region of a cross section of the elytra of *Thymalus* in the region immediately posterior to the metathorax.   × 130.

2. Fig. 10 shows in cross section the thickened edges of the elytra, and the metathoracic groove (*g*) into which they hook.

The hooks are so pronounced that they make a very perfect joining, which holds the edges of the elytra together along the dorsal suture.   This arrangement is made more effective by rows of minute chitinous teeth (*o*, *p*) which in the cross section resemble saw teeth.   These are so directed that they keep the elytra from slipping laterally when they are being drawn together, by interlocking at the points *q* and *q'* they assist in keeping the wing covers perfectly co-adapted when at rest.

3. The interlocking of the elytra of *Thymalus* along their anterior edges is very much as it is in *Lachnosterna*.   The principal difference is that the inner anterior corners of the elytra slip under the scutellum more than in the June beetle and the pronotum fits against the anterior edges more firmly.

4. The method of fastening the elytra to the meta-episternum is shown in Fig. 9.   This figure is copied from Breed (:03, Fig. 13, Plate 6).   A description of the mechanism which it illustrates is to be found on page 332 of the paper referred to.   There is a ridge (*pli.*) on the face of the episternum, lying between the attachments of the musculus episternalis (*e'stn.*).   The contraction of this muscle causes the ridge (*pli.*) to take the position indicated by the dotted line, thus freeing the ridge (*loph.*) on the elytron and allowing the latter to be raised.   In like manner the musculus episternalis contracts when the elytron returns to rest and its immediate relaxation causes the latter to be securely fastened in its place.   At the point marked by a star (*) there is found on the inner face of the elytron a row of minute teeth directed upward.   A similar series of teeth pointing downward is found on the body wall opposite.   These teeth interlock and assist in keeping the elytron in place.   A few small teeth are also present on the inner face of the ridge (*pli.*).

The dorsal suture is thus kept intact by the combined working of the dorsal metathoracic groove and this lateral hooking arrangement.   The combination of these two devices produces the stress which holds the mid-dorsal edges of the elytra in the positions shown in Figs. 10 and 11.

(c) *Interlocking Mechanisms found in Tenebrio.*

The common meal beetle is one of the Tenebrionidæ. It may be found abundantly through the summer months in granaries and mills, or flying into houses. It is an elongated beetle whose head, prothoracic and body regions are distinctly separated from each other in dorsal view.

The elytra of this beetle are not very firmly interlocked either with the body or with each other. All four of the methods previously mentioned are used in this interlocking.

1. The mid-dorsal edges of the elytra are co-adapted much as in *Lachnosterna* (cf. Fig. 1). However minute teeth are found along the dorsal surface of the ridge c, which fit in with similar teeth on the ventral side of the ridge b. In three of the individuals examined the ridge on the right elytron fitted into a groove on the left elytron while in two others the reverse was true.

2. The dorsal groove along the metathorax is both shallow and narrow. Minute interlocking teeth are developed on the thickened edges of the elytra and on the metathorax, as in *Thymalus* (cf. Fig. 10). These teeth are more blunt than those in *Thymalus* and do not form as perfect an interlocking device.

3. The inner anterior corners of the elytra slip under the diagonal edges of the scutellum, showing very perfect co-adaptation at this point. The prothorax does not fit tightly against the elytra and is not used in holding them in place.

4. The most interesting of these co-adaptations is that of the lateral edges of the elytra with the episternum. As seen in Fig. 12, which represents the right lateral portion of a cross section through this region viewed from behind, there are numerous teeth on the inner surface of the elytron at s, which interlock with teeth on the body wall at s'. Apparently the teeth at t and t' do not interlock because: (1) long movable hairs are found along the small ridge u, which would interfere with this action; (2) the shape of the body would prevent it; (3) the teeth themselves do not seem stout enough to serve for this interlocking. The action of the teeth at s and s', working in connection with the co-adaptations along the dorsal suture, would cause a strain on the elytra which would hold them in place.

The triangular area embraced between the straight dotted lines shows the form of the episternal muscle projected on the plane of the section. The origin of the musculus episternalis is along the entire dorsal boundary of the meta-episternum. Most of its fibers take their origin from the thickened ridge v. The insertion is by means of a tendon which attaches to the anterior portion of the ventral edge of the episternum. The entire muscle is thus
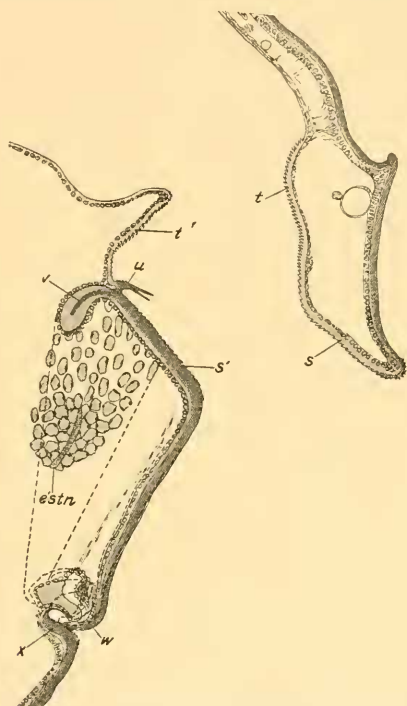

FIG. 12. Lateral portion of a cross section of the metathorax of *Tenebrio*, show-ing the parts affected by the contraction of musculus episternalis. $\times 75$.

somewhat fan-shaped in side view. It is only in sections anterior to the one shown that the fibers are cut so as to show their full length in any one section.

It is difficult to determine the exact method by which the muscle operates. The structure of the suture to which this mus-cle attaches is remarkably complex and entirely unlike that found in the two beetles just described. The structure shown in Fig. 12 is typical for all of the sections of this suture The teeth shown

along the outer surface of the region w and the surface x show a better development in the section figured than in most of the sections.

There are at least two reasons for thinking that the condition figured is one which represents the contracted or nearly contracted state of this muscle. These reasons are : (1) the cross striations of the muscle appear as they do in contracted fibers, (2) the position of the parts affected. A dotted outline has been drawn (not shown satisfactorily in the figure) which indicates the probable position of these parts when the muscle relaxes. This relaxation would cause the teeth at s and s' to grip each other firmly if the elytron had previously been brought near enough the body for these surfaces to touch each other.

The most effective of the interlocking devices in this beetle are the mid-dorsal metathoracic groove, the slipping of the corners of the elytra under the scutellum, and the interlocking of these teeth along the meta-episternum.

(d) Comparison.

A comparison of the devices which are used by these beetles in holding their elytra in place reveals a close similarity in all cases, except in the interlocking of the lateral edges with the meta-episternum. Here the most striking dissimilarity exists. In all of the beetles which we have examined, a muscle has been found which originates along the dorsal edge of the episternum, and is inserted on the suture which marks the ventral boundary of this plate. This has been called the musculus episternalis. In one case (*Lachnosterna*) this muscle is apparently functionless since the chitinous structures which it operates are so degenerate that they no longer interlock. In *Thymalus* this muscle operates an upward hooking ridge, in *Tenebrio* a series of downward hooking teeth.

This dissimilarity of structure with its consequent differences in the method of operation is made possible by varying flexibilities of the chitinous cuticula.

It would be interesting to know how many other variations of these structures may be present among beetles. The three species examined were chosen at random and it does not seem possible

that all of the variations have been discovered.   Some light might be thrown on the relationships of the various families of beetles to one another if more were known about these interlocking devices.

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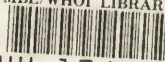'98   A Text-book of Entomology.   New York, xvii + 729 pp., 654 figs.

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